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Quantitative Gene Action and Interrelationships of Protein Content With Some Metrical Traits of Oats

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QUANTITATIVE GENE ACTION AND INTERRELATIONSHIPS
OF PROTEIN CONTENT WITH SOME
METRICAL TRAITS OF OATS

BY

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Under the supervision of Dr. Dale L. Reeves

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Four genetically distinct cultivars with protein content ranging from 15.7 to 26.6 percent were crossed in all possible combinations to make a complete set of diallel crosses. The data suggested additive gene action and partial dominance for protein content. Groat percentage and number of panicles showed overall partial dominance. Yield and days to heading indicated over-dominance, whereas height, plant weight and groat weight exhibited complete dominance. A. sterilis manifested dominance for early heading, low groat percentage and a large number of panicles. It exhibited recessiveness for yield, plant weight and groat weight.

Narrow sense heritability for protein content varied from 41 to 83 percent while broad sense heritability ranged from 0 to 98 percent

depending on genotype, environment and method used for computation. Genotype x environment interactions for protein content were significant.

Frequency distribution for protein content in the F_3 generation was reasonably symmetrical. Mean protein content was skewed toward the low protein content. F_3 progeny from a cross involving two low protein parents had a lower average protein percentage than either parent. Some crosses had progeny with as high as 25 percent protein and yield above the mid-parent value were observed.

Number of effective factors controlling protein content varied from 1 to 19, depending upon the method of determination and genetic diversity of the parents.

Protein content exhibited negative correlations with yield, plant weight, height, number of spikelets, groat percentage, leaf length, leaf width and days to heading. A positive correlation of protein content was observed with awns, which is a *A. sterilis* characteristic.

On the basis of standard partial regression coefficients, number of spikelets and yield were the most influential variables to predict protein content in the F_1 and F_3 generations, respectively. To predict yield, plant weight and number of spikelets were the best factors.

There was a constancy of generation means for protein content in the F_1, F_2 and F_3 generations. General combining ability, specific combining ability and reciprocal effects were significant in the F_1 generation for protein content.

Based upon this study, it can be concluded that the high protein content of *A. sterilis* can be combined with agronomic traits of *A. sativa*. This might be achieved by selecting from large populations of segregating material followed by backcrossing to *A. sativa* to recover better agronomic traits.

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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Doctor of Philosophy, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Thesis Adviser | Date

Head, Plant Science Department | Date

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On the basis of standard partial regression coefficients, number of spikelets and yield were the most influential variables to predict protein content in the F_1 and F_3 generations, respectively. To predict yield, plant weight and number of spikelets were the best factors.

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TABLE OF CONTENTS

Page

LIST OF TABLES

Table		Page

Table		Page

LIST OF FIGURES

Figure		Page

INTRODUCTION

The rapidly increasing human population is creating a demand for more and more food. Due to ultimate limits on agricultural land and resources, the ability of mankind to feed itself in the future seems to be questionable. Modern agriculture can meet the caloric requirements at the present time, but a good quality diet which contains adequate proteins with the proper amino acid balance is also important for physical and mental functioning.

Cereals are the major source of energy and proteins for a vast majority of the world population. This is more true in the countries where animal proteins are scarce in the diet. Among common cereals in the United States, oats rank highest in both protein and the limiting amino acid lysine (42). Oats have been proven to be an excellent breakfast cereal with better protein digestibility and nitrogen retention rate than other cereals (30). Use of oats as livestock feed is maintaining popularity due to comparatively low cost and high nutritive value.

Improvement of protein quality and quantity by genetic means seems to be the most promising approach. There is enough genetic diversity in oat protein content (12-24 percent) to manipulate this trait. Avena sterilis L., a wild oat collected in Israel, runs still higher (up to 30 percent) in protein and also carries genes for resistance to some crown rust races. Exploitation of this species appears likely to make some progress due to the ease in crossing with cultivated oats having the same number of chromosomes. A. sterilis, as such, cannot be used for cultivation due to low yield, shattering and presence of large awns.

Increasing protein content by sacrificing yield would not be a worthwhile proposition. A coordinated approach to combine the desirable traits of A. sterilis with commercially grown genotypes is needed. Progress in this direction is dependent on the availability of genetic information and efficient breeding techniques. This study was undertaken with the following specific objectives:

1. To determine the type of gene action, heritability and number of effective factors controlling protein content.

2. To study the relationship of protein content with other agronomic traits.

3. To evaluate the feasibility of utilizing A. sterilis germplasm in oat breeding projects.

REVIEW OF LITERATURE

After understanding the nutritional impact of protein on diet, some efforts have been oriented towards raising the protein level of cereal grains. Several studies conducted over the last 50 years have revealed that protein content in corn and wheat is under genetic control, although environment exerts strong influence in the expression of this trait (10, 16, 23, and 24).

Inheritance of Protein Content in Cereals

A genetic study on the protein content of corn was reported by Hayes and Garber (24). They increased protein content through recurrent selection. Later, East and Jones (16) postulated that several loci controlled protein content in corn grain. Clark (10) reported on the inheritance of wheat protein, however he did not find any segregate which had greater protein content than its high parent. He indicated no dominance for high protein percentages and the inheritance of protein was complex due to the fact that environment affected its expression. Haunold *et al.* (23) found that F_2 plants and F_3 lines in wheat crosses were intermediate in protein content between parents. Highly significant positive correlations for protein in the grain of F_2 plants and of F_3 progeny rows were reported. Lebsock *et al.* (31) reported partial dominance for low protein in a wheat cross and detected genotype x environment interactions. Stuber *et al.* (46) indicated significant negative correlation between yield and protein content in wheat. Briggs *et al.* (3) showed a positive correlation between yield and protein content in wheat. They suggested that in areas of nitrogen deficiency, both yield and protein level are adversely affected by a lack of soil fertility.

Davis et al. (13) estimated broad sense heritabilities ranging from 54 to 60 percent in four wheat crosses and narrow sense heritabilities of 88, 89 and 90 percent in three different oat crosses. They concluded that partial dominance for low protein content was present. Campbell and Frey (8) crossed *Avena sterilis* with *A. sativa* and found the protein content to be intermediate to the parents. They suggested additive gene action for protein content in oats. Heritability estimates were 41, 57 and 30 percent using mean per plot, per experiment and regression method, respectively. Ohm and Patterson (41) also studied *A. sterilis* by *A. sativa* crosses for protein content. They concluded that F_1 hybrids produced a lower percent groat protein than the mid-parental value. Percent groat protein was maintained from F_1 to F_2. Partial dominance for low protein was indicated. High percent groat protein was recessive in all crosses. Murphy et al. (39) observed some transgressive segregation in the F_2 generation following a cross of *A. sativa* and *A. sterilis*. Heterosis for groat weight was noted. Frey (17) studied two corn crosses for protein inheritance and concluded that low protein percentages were dominant.

Woodworth et al. (50) applied long term selection on corn for high and low protein and suggested that many genes were involved, with predominantly additive gene action controlling protein content. In 50 generations of selection, the protein content was changed from 10.9 percent in the original population to 19.5 percent in the high population and 4.9 percent in the low population. There was still variability for protein content after 50 cycles of selection.

Jenkins (27) crossed _A_. _sativa_ with _A_. _byzantina_ and found that the highest yielding segregates had average or slightly better than average values for nitrogen content. In the F_1 trial there was a marked heterosis for grain yield (28).

Character Association with Protein

Campbell and Frey (7) found high groat protein percentages closely associated with abscission spikelet separation and jointed awn, both of which were _A_. _sterilis_ type. Shattering and dark seed color were also associated with high groat protein percentages, but kernel pubescence did not indicate high protein. Spilde (45) also found that high protein content was associated with the _A_. _sterilis_ phenotype. Ohm and Patterson (40) studied a six-cultivar diallel for protein in _A_. _sterilis_ and found that the relationship between yield and protein tended to be negative but not statistically significant. However, a high negative correlation between yield and protein was found by Brown _et al._ (4) and Spilde (45). On the other hand, Jenkins (28) studied _A_. _sativa_ and _A_. _byzantina_ crosses and reported a positive correlation of yield of grain crude protein with grain yield.

Hutchinson and Martin (26) observed a negative correlation between yield and grain nitrogen content grown under different environments. They found that poorly filled grain with very high nitrogen content was produced when oats ripened prematurely.

Wiggans (49) reported an influence of number of fertile spikelets on a panicle on the protein percentage of oat grain. Kernels in blasted oat panicles contained approximately 0.5 percent higher nitrogen percentage than normal panicles. Hutchinson and Martin (26) reported an inverse relationship between oil content and nitrogen content. Brown et al. (4) observed a similar relationship in spring and winter oats.

Environmental Influence on Protein Content

Middleton et al. (36) analysed 15 varieties of oats for protein content grown in nine locations and found highly significant differences between varieties, locations and variety by location interactions. Lebsock et al. (31) observed genotype x environment interactions in wheat. Ohm and Patterson (40) also concluded that environmental factors were important in protein yield. Ashton (1) indicated that when grains were poorly filled they had a higher percent of crude protein. Murphy (38) found consistent increase in protein content of oats as a result of infection with crown rust *Puccinia coronata* Cda. f. sp. *avenae*.

Nitrogen fertilizers have increased protein content in sorghum (Waggle et al., 48), corn (Saukerlick et al., 44), barley (McBeath et al., 34) and oats (Portch et al., 43). MacGregor et al. (32) reported that protein content and total amino acids were increased with nitrogen fertilizers on corn. Campbell and Picket (6) reported a decrease in protein quality with the increase of percent protein and yield in sorghum. Briggs et al. (3) pointed out nitrogen deficiency as a limiting factor of grain protein content and yield of wheat.

MATERIALS AND METHODS

Experimental Materials

The four oat cultivars used in this study are listed in Table 1, with their C-I numbers and pedigrees. Three of these cultivars, i.e., 'Spear' (SD), 'Kelsey' (KL) and 'Roxton' (RX) are commercially grown varieties belonging to *Avena sativa* L. and the fourth one is an *Avena sterilis* L. (AS) collection from Israel. Crosses were made in all possible combinations to form a complete diallel. The F_2 and F_3 generations were grown at the Agronomy Farm at Brookings, South Dakota and the Sioux Valley Research Farm at Watertown, South Dakota. The term 'F_1 generation' is used here in the sense that information was obtained from F_1 plants and its parts, although seed derived from these plants was genetically F_2 seed. Hereafter the cultivars will be identified by their designations as shown in Table 1. Handling of the material is discussed separately under each generation.

F_1 Generation

The soilbed in the greenhouse was formed into ridges about 20 cm high, five meters long and 50 cm apart. F_1 seeds of all 12 crosses and four parents, previously germinated on filter paper, were transplanted on the ridges, 10 cm apart. During the summer period, the greenhouse was kept cool by shading with a thick solution of wheat flour and by the use of fans. Seeds of *A. sterilis* were hand-picked at ripening. The following data were obtained for each plant:

Table 1. C.I. numbers, pedigrees and designations of parental cultivars used in this study.

C.I.number	Cultivar	Designation	Pedigree
9203	Spear	SD	Neal/Clintland 64
8171	Kelsey	KL	Victoria/2/Hajira/Banner/3/Roxton/4/Beacon/5/Rodney
4134	Roxton	RX	Siberian/Joanette/2/OAC72/Early Ripe
-	*Avena sterilis* L. var. *maxima* Perez Lara	AS	AS 6-76

1. Days to head. Days from the date of transplanting until the emergence of the first panicle.

2. Plant height. The height in centimeters from the ground to the tip of the tallest panicle.

3. Leaf length. Length in centimeters of the leaf blade of the second leaf from the top, at heading stage.

4. Leaf width. The width in centimeters at the middle of the second leaf blade.

5. Number of panicles. Total number of panicles per plant.

6. Number of spikelets. Number of fertile spikelets per plant.

7. Yield. Kernel yield in grams per plant.

8. 20 groat weight. The weight to the nearest ten-thousandth of a gram of 20 groats taken at random from each plant.

9. Protein percent of groat. Standard Kjeldahl method.

10. Groat length. The length of the groat in mm, measured with a Filar micrometer[1] eyepiece attached to a stereomicroscope.

F_2 Generation

Seeds from F_1 plants were bulked within the cross. Some F_2 plants were grown in the greenhouse (pots placed on benches) during the fall of 1972 to advance one generation. The F_2 generation was planted at

[1]Obtained from American Optical Corporation, Buffalo, N. Y.

Brookings on April 10, 1973 and at Watertown on April 23, 1973. About 20 F_2 seeds per cross were space planted 10 cm apart in a row of two meters long and 30 cm apart. Rows were randomized within the group of 16 genotypes, including the four parents. Three replications were grown at each location. Two border rows were planted around each block of 16 genotypes. A heavy string was stretched around each row to keep plants from lodging. On July 4, 1973, (at the milk stage) 'Arasan' was sprayed on the plants to deter birds.

A. sterilis and its progeny were bagged on July 5, 1973 to hold the kernels of shattering genotypes. "Glycine" bags (10 cm x 5 cm x 30 cm) were used for this purpose with 12 holes each, five mm in diameter to permit ventilation. Plants were harvested individually on July.20, 1973 and kept dry until threshed. Threshing was done with a head thresher operated at medium speed.

Most of the data were recorded in the same way as for the F_1. Weight of 50 groats was recorded instead of 20 groats. Groat length and groat breadth were not measured in the F_2. Groat percentages were determined by weighing about five gm of the kernels and then running them through a small modified Quaker Oats impact dehuller and a small sample cleaner. The remaining debris was picked by hand. Final weight of the groats was recorded and the ratio of groat weight to total kernel weight was computed. Plant weight was determined by cutting the whole plant at the ground level, drying and then weighing to the nearest gram.

F_3 Generation

Seeds from the F_2 plants that were grown in the greenhouse during the fall of 1972 were used to plant the F_3 generation in the field at Brookings and Watertown on July 10 and July 23, 1973, respectively. The F_3 generation was grown in hill plots as described by Frey (20). Hills were spaced 30 cm between and within rows. There were 25 hill plots planted with the progeny of each cross. Two hill plots of each of the parents were interpersed within the row. Crosses were randomized within each block. There were four replications at each location.

A push type Columbia-planter with attached funnel was used for planting. The planter was stopped on previously marked hills and 11 seeds were poured through the funnel. The seeds were spread over an area of approximately five cm in diameter within the hill. Bamboo stakes were used to keep plants from lodging. A. sterilis and its progenies were covered with transparent plastic bags (13 cm x 10 cm x 33 cm) to hold the shattering kernels. There were 12 holes, 5 mm in diameter made in each bag to allow ventilation. Most of the note taking was the same as in F_1 and F_2 generations except each hill plot was considered an experimental unit, instead of single plants. Harvest indices were calculated by dividing kernel yield by total above ground plant dry matter.

Soil samples were taken at the time of planting at both locations. Data for soil tests, monthly average temperature and precipitation are given in Appendix 1.

Protein Analysis in the F_2 and F_3 Generations

Protein analysis was done by the USDA National Oat Quality Laboratory at Madison, Wisconsin. They used the dye-binding method as described by Udy (47). The standard Kjeldahl method was employed as a periodic check. The dye-binding technique is based on the ability of 'Acid-Orange-12' dye to bind with three basic amino acids in cereal proteins. Ground oat groats, 480 mg from a three gram sample, were shaken in 40 ml of the dye for 50 minutes. Samples were then centrifuged and light transmission of the dye solution was read at 480 nm. A correlation coefficient of 0.960 between the Udy and Kjeldahl methods has been reported by Youngs et al. (51). The two methods differed by only 0.2 percent in the measurement of protein of 587 samples taken at random. Amino acids, starch and fat analysis were done at the Quaker Oats Research Laboratory at Barrington, Illinois.

Statistical Procedure

Analysis of variance was computed for a randomized complete block design. Stepwise multiple regression coefficients were transformed into standard partial regression coefficients and characters were ranked according to value. Heritability was estimated by using two methods:

Heritability estimates:

Method 1. Mahmud and Kramer (33).

$$h^2 = \frac{VF_2 - [(VP_1 \cdot VP_2)]^{\frac{1}{2}}}{VF_2}$$

h^2 = Heritability
VF_2 = Variance of the F_2 generation
VP = Variance of the parent

Method 2. Burton (5).

$$h^2 = \frac{VF_2 - VF_1}{VF_2}$$

Estimates of effective factors:

Castle (9).

$$n = \frac{D^2}{8(\sigma F_2 - \sigma F_1)}$$

n = Number of effective factors
D = Difference between parental means
σ = Standard deviation

Mather and Jinks (35).

$$K_1 = \frac{(\overline{P}_1 - \overline{P}_2)^2}{4HV}$$

K_1 = Number of effective factors
HV = H_2 = Heritable portion of variation
$\overline{P}$ = Mean of the parent

Estimates of genetic components of variation were obtained after Jinks (29) and Hayman (25). Values of (Vr, Wr) graphs were plotted. Procedures used are also described along with the results.

EXPERIMENTAL RESULTS

Data pertaining in the F_1 and F_2 generations were taken on individual plants and in the F_3 generation on hill plots. These data have been summarized for population means, variances, correlations and standard partial regression coefficients. Gene action is discussed on the basis of data obtained in the F_2 generation grown at Brookings, South Dakota. Major emphasis will be placed on protein content.

The experimental material was under some moisture stress, as the rainfall was below average (see Appendix 1). Insects and crown rust were not a problem during the growing season. Halo blight patches were seen after the first week of June, 1973.

The results are presented in this sequence: Parents, F_1, F_2 and F_3 generations.

Parents. Pedigrees, C.I. numbers and designations of the parental genotypes are given in Table 1. Chemical composition and means of characters studied are given in Tables 2 and 3, respectively.

Spear (SD 955). This cultivar was used as a high protein parent among *A. sativa* genotypes. 'Spear' has been recently released as a commercial variety. It has consistently given above 20 percent protein over the past few years. It is a midseason variety of medium height with reasonably good yield.

Kelsey. This is a high yielding variety that is well adapted under eastern South Dakota conditions. Kelsey has low protein content (approximately 15 percent).

Table 2. Chemical composition of four oats parents

component	ROXTON	SD955	KELSEY	Avena sterilis
Fat percent	6.2	6.3	6.3	8.7
Starch percent	53.1	51.0	56.0	45.7
Protein percent	15.4	20.3	14.4	24.3
Amino acid(% of Proteins)				
Lysine *	4.37	4.20	4.34	3.94
Histidine *	2.28	2.41	2.28	2.28
Ammonia	3.30	3.45	3.37	3.37
Arginine *	7.03	7.16	6.97	6.73
Aspartic acid	8.19	8.76	8.23	7.87
Threonine *	3.01	2.88	2.94	2.84
Serine	3.75	3.45	3.58	3.27
Glutamic acid	22.35	22.75	22.37	23.92
Proline	5.38	5.38	5.43	5.34
Glycine	5.31	4.99	5.29	4.82
Alanine	4.89	4.84	4.95	4.56
Half Cystine	1.29	0.96	1.20	0.81
Valine *	6.00	5.92	6.10	6.49
Methionine *	1.91	1.56	1.57	2.00
Isoleucine *	4.16	4.37	4.31	4.69
Leucine *	8.10	7.86	8.18	8.71
Tyrosine	3.43	3.45	3.31	3.02
Phenylalanine *	5.28	5.62	5.17	5.34

* Essential amino acids

Roxton. This is an old variety released in Canada. It is one of the parents of Kelsey. It is very tall and late with low protein content (16 percent).

Avena sterilis L. This is a wild species collected in Israel. It is distinct from *A. sativa* in several ways, such as large awns, shattering habit, pubescence and a large number of panicles with fewer spikelets on each panicle. The selection used had high protein content and resistance to some crown rust races.

The chemical composition of the parents in Table 2 gives a clear picture of the quality of the parental genotypes. There is a good amino acid balance as the essential amino acids constitute approximately 42 percent of the protein in the groats of *A. sativa* parentage Starch content varied with the proteins indicating an inverse relationship.

F_1 Generation

Means of the F_1 generation are given in Table 3. Protein content of the F_1 derived groats show a range from 14.5 to 25.6 percent, depending upon the genotype involved. All the F_1 hybrids except 'AS' x 'SD' and 'AS' x 'KL' had a protein content below the mid-parent value. Some genotypes showed heterosis in yield as they exceeded their high parent. Reciprocal differences were seen for protein content as depicted in Tables 4-8. All genotypes were significantly different at the 0.01 level of probability for protein percent, days to head,

Table 3. Parent and cross means, grand means and coefficients of variability in the F_1 generation.

Population	Yield (gm/plant)	Protein percent	20 groat weight (gm)	Groat length (mm)	Groat breadth (mm)	Days to head	Height (cm)	Panicle number	Spikelet number	Leaf length (cm)	Leaf width (cm)
A S	1.0	26.6	0.3138	8.55	1.91	41	102	31	40	20.3	0.9
S D	7.9	20.5	0.4017	7.05	2.45	36	107	7	114	29.3	1.6
K L	9.6	15.9	0.3982	6.81	2.42	39	135	7	160	29.7	1.9
R X	12.1	15.7	0.3837	7.67	2.05	45	174	9	216	35.2	2.0
KL x AS	10.2	18.4	0.3812	7.69	2.26	34	147	11	113	26.7	1.4
KL x SD	9.6	16.0	0.4090	7.04	2.42	35	131	6	185	28.2	1.7
KL x RX	14.9	14.7	0.4014	7.42	2.28	43	148	9	209	36.9	2.0
RX x AS	9.6	18.8	0.3969	7.97	2.28	39	151	13	80	30.1	1.4
RX x KL	7.6	14.5	0.4885	7.41	2.43	38	140	6	214	33.5	1.9
RX x SD	11.5	17.7	0.4319	8.07	2.58	38	142	7	171	31.0	1.6
SD x AS	7.3	23.7	0.3567	7.41	2.20	35	130	11	65	25.4	1.1
SD x KL	8.7	16.8	0.4934	7.91	2.61	36	128	7	127	24.7	1.5
SD x RX	10.8	16.7	0.4806	7.58	2.53	36	126	7	116	28.5	1.5
AS x SD	1.4	25.6	0.3678	7.48	2.11	47	95	20	37	18.5	0.8
AS x KL	1.9	22.7	0.4462	8.70	2.36	35	97	25	41	19.7	0.8
AS x RX	2.0	20.8	0.4263	8.39	2.29	33	109	16	41	20.2	0.7
Grand mean	9.3	18.4	0.4075	7.56	2.35	38	134	10	130	28.6	1.5
C.V. (%)	52	18	16	10	18	12	16	60	46	21	28

Table 4. F_1 means, midparent values, deviations, and reciprocal differences for protein content in F_1 generation.

Population	F_1 mean ($\bar{F}_1$)	Midparent value ($\bar{P}$)	Deviation ($\bar{F}_1$-$\bar{P}$)	Reciprocal difference
KL x AS	18.4	21.4	-2.9	4.3
KL x SD	16.0	18.2	-2.2	0.8
KL x RX	14.7	15.8	-1.1	0.2
RX x AS	18.8	21.2	-2.8	2.0
RX x KL	14.5	15.8	-1.4	0.2
RX x SD	17.7	18.1	-0.4	1.0
SD x AS	23.7	23.6	+0.1	1.9
SD x KL	16.8	18.2	-1.4	0.8
SD x RX	16.7	18.1	-1.4	1.0
AS x SD	25.6	23.6	+2.0	1.9
AS x KL	22.7	21.4	+1.4	4.3
AS x RX	20.8	21.2	-0.4	2.0

Table 5. Mean squares from analysis of variance of eleven traits in F_1 generation.

Source of variation	d.f.	Protein percent	Yield (gm/plant)	Days to head	Height (cm)	20 Groat weight	Panicle number
Replications	1	0.01	10.91	49.98 **	295.69	0.000	48.21 *
Genotypes	15	106.04 **	112.30 *	135.73 **	3796.04 **	0.017 **	294.82 **
G x R	15	2.14 *	17.86	15.67 **	105.61	0.001	24.60 **
Error	134	1.23	14.45	6.21	91.03	0.003	9.62

Source of variation	d.f.	Spikelet number	Groat length (mm)	Groat breadth (mm)	Leaf length (cm)	Leaf width (cm)
Replications	1	48.14	0.008	0.023	35.59	0.076
Genotypes	15	32688.02 **	2.424 **	0.322 *	207.96 **	137.012 **
G x R	15	179.11	0.324	0.107	23.76	4.244
Error	134	931.15	0.395	0.166	17.67	7.031

*Significant at .05 level. ** Significant at .01 level.

20 seed weight, panicle number, spikelets, groat length, leaf length and leaf breadth. Yield and groat breadth were significant at the 0.05 level. A genotype x replication interaction was significant in protein content at the 0.05 level of probability, days to head and panicle number at the 0.01 level.

Character Association

Protein showed a negative relationship with 20 seed weight, groat breadth, height, number of spikelets, leaf length and width and yield (Table 6). Yield had a negative correlation with the number of panicles at the 0.01 level of probability. Significant positive correlations of yield were noted with groat breadth, plant height, number of spikelets, leaf length and width. The only positive relationship of protein content was with the number of panicles and groat length.

Standard partial regression coefficients determined by stepwise multiple regression indicated that the number of spikelets was the most important character to predict protein content followed by plant height, 20 groat weight and the number of panicles (Table 7). Standard partial regression coefficients for yield show that the number of spikelets, plant height and groat breadth were very important variables to predict yield (Table 7).

Analysis of the F_1 data using Griffing's Method 1, model 1, diallel analysis depicted highly significant differences for general combining ability, specific combining ability and reciprocal effects

Table 6. Simple correlation coefficients among eleven characters in the F_1 generation.

	Yield	Protein percent	20 Groat weight	Groat length	Groat breadth	Days to head	Height	Panicle number	Spikelet number	Leaf length
Protein percent	-0.564**									
20 Groat weight	0.057	-0.247**								
Groat length	-0.081	0.247**	0.293**							
Groat breadth	0.263**	-0.163*	0.276**	0.048						
Days to head	0.050	-0.104	-0.112	0.025	-0.136					
Height	0.548**	-0.532**	-0.043	-0.021	-0.091	0.269**				
Panicle number	-0.339**	0.581**	-0.241**	0.317**	-0.207**	0.108	-0.228**			
Spikelet number	0.657**	-0.757**	0.058	-0.243**	0.093	0.227**	0.545**	-0.463**		
Leaf length	0.430**	-0.531**	0.052	0.161**	-0.003	0.303**	0.510 **	-0.369**	0.542**	
Leaf width	0.469**	-0.657**	0.114	-0.233**	0.105	0.273**	0.443**	-0.467**	0.671**	0.726**

* significant at .05 level ** significant at .01 level

Table 7. Rank of character influence upon yield and protein content as determined on the basis of standard partial regression coefficients in the F_1 generation.

Character	Standard partial regression coefficient
Dependent variable: PROTEIN	
Independent variables :-	
Spikelet number	-0.4161 (1)
Plant height	-0.2055 (2)
20 groat weight	-0.1880 (3)
Panicle number	0.1687 (4)
Leaf width	-0.1632 (5)
Groat length	0.1047 (6)
Days to head	0.0440 (7)
Groat breadth	-0.0335 (8)
Yield	-0.0185 (9)
Leaf length	0.0013 (10)
Dependent variable: YIELD	
Independent variables :-	
Spikelet number	0.4739 (1)
Plant height	0.3049 (2)
Groat breadth	0.2445 (3)
Days to head	-0.1388 (4)
Leaf length	0.0784 (5)
20 groat weight	-0.0628 (6)
Groat length	0.0600 (7)
Protein percent	-0.0282 (8)
Panicle number	0.0194 (9)
Leaf width	-0.0180 (10)

for protein content (Table 8). Yield showed highly significant differences for general combining ability and reciprocal effects.

Estimates of general combining ability, specific combining ability and reciprocal effects are given in Table 9 for protein and yield. 'AS' showed the highest general combining effect for protein, followed by 'SD'. 'KL' and 'RX' had a negative general combining ability effect for protein. The effects for yield were just the opposite (Table 9). Specific combining effects for protein in 'AS' were negative while the other three genotypes were positive, 'RX' being the highest. Such effects for yield were reversed for protein. Positive values of reciprocal effects for protein indicated that there were differences as to the reciprocity of the cross. Cross 'SD' x 'RX' showed a negative value. Yield showed negative reciprocal effects in all crosses except 'KL' x 'RX'.

F_2 Generation

Means, grand means and coefficients of variation are given in Table 10 for two locations. Protein percentages were higher at Watertown as compared to Brookings. Similar trends were observed in yield, plant weight and 50 groat weight.

The analysis of variance in Table 11 depicted significant differences among genotypes in protein content, yield, plant weight, days to head, panicles, height, groat percent and 50 groat weight. Mean squares for replications were significant at the 0.01 level of probability for protein percent, days to head, height, groat percent and 50 groat weight.

Table 8. Diallel analysis for protein content and yield.(Griffing Method 1. Model 1. 1956). Analysis of Variance.

ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Mean squares PROTEIN	Mean squares YIELD
General combining ability (G.C.A.)	3	67.07**	70.03**
Specific combining ability (S.C.A.)	6	1.58**	0.88
Reciprocal effects	6	2.16**	24.90**
Error	128	0.128	0.722

** Significant at 0.01 level of probability

Table 9. Estimates of general combining ability, specific combining ability and reciprocal effects for protein and yield of four parents.

A. Estimates of GENERAL COMBINING ABILITY:

Parent	protein	yield
A S	3.86	-3.58
S D	0.57	0.25
K L	-2.23	1.13
R X	-2.20	2.19

B. Estimates of SPECIFIC COMBINING ABILITY:

A S	-0.031	0.281
S D	0.053	-0.493
K L	1.078	-0.543
R X	1.233	-0.168
AS x SD	1.151	-0.206
AS x KL	-0.096	0.618
AS x RX	-0.023	-0.693
SD x KL	-0.988	-0.118
SD x RX	-0.216	0.818
KL x RX	0.006	0.043

C. Estimates of RECIPROCAL EFFECTS :

AS x SD	0.965	-2.950
AS x KL	2.115	-4.150
AS x RX	0.840	-3.800
SD x KL	0.375	-0.450
SD x RX	-0.480	-0.350
KL x RX	0.060	3.650

Table 10. Parent and cross means, grand means and coefficient of variability at Brookings and Watertown in the F_2 generation.

		Protein percent	Yield (gm/plant)	Plant weight (gm/plant)	50 Groat wt. (gm)	Panicle Number	Height (cm)	Days to Head	Groat percent
AS	B*	23.5	3.5	8.8	0.8144	6.0	78.0	64	53.7
	W**	24.4	1.9	4.6	0.7338	4.6	76.8	63	61.5
SD	B	20.7	6.1	12.2	1.0929	4.5	72.7	63	75.3
	W	23.5	5.0	9.9	0.9718	3.8	80.6	61	75.5
KL	B	14.5	8.8	17.7	1.1720	4.0	86.9	69	76.5
	W	15.1	5.5	11.0	1.1069	3.7	86.6	64	77.9
RX	B	15.6	7.7	17.5	1.1887	3.0	101.3	71	74.0
	W	16.0	5.4	11.9	1.2397	3.0	93.5	68	75.3
KLxAS	B	18.7	7.4	15.0	1.1066	4.8	92.2	64	63.8
	W	20.9	4.8	9.8	0.9640	4.9	92.4	60	64.4
KLxSD	B	17.3	8.4	16.6	1.2272	4.2	86.4	66	71.8
	W	19.6	6.4	12.1	0.9814	3.9	84.9	63	74.1
KLxRX	B	14.5	12.0	21.3	1.3233	3.6	96.5	69	72.0
	W	15.9	6.3	13.4	1.2003	3.6	94.5	66	75.6
RXxAS	B	19.7	6.5	14.8	1.1925	5.0	97.0	63	63.4
	W	20.9	4.2	9.6	1.1083	4.4	96.5	60	67.9
RXxKL	B	14.6	9.5	19.6	1.2836	3.5	95.2	69	71.9
	W	16.3	6.2	13.2	1.1999	3.4	94.2	64	76.5
RXxSD	B	17.6	9.2	18.8	1.2130	3.7	94.0	67	72.8
	W	18.5	7.0	14.2	1.1005	3.7	91.4	64	74.5
SDxAS	B	22.6	6.9	14.3	1.0271	6.2	90.6	64	60.2
	W	24.5	5.4	10.7	0.9906	5.4	90.4	60	67.8
SDxKL	B	17.6	8.4	16.7	1.1849	4.4	83.2	63	72.7
	W	19.1	5.6	10.8	1.0098	3.8	82.7	61	75.2
SDxRX	B	17.8	8.7	18.8	1.2764	4.1	88.3	65	77.8
	W	19.5	6.5	13.1	1.1571	3.7	93.0	63	75.0
ASxSD	B	21.3	6.2	12.7	1.0979	5.0	84.2	64	67.1
	W	24.3	4.8	9.5	0.9989	5.1	84.4	61	65.2
ASxKL	B	18.8	7.5	15.3	1.1768	5.7	86.2	63	68.8
	W	20.3	5.4	10.8	0.9753	5.5	87.4	59	64.8
ASxRX	B	19.6	7.2	16.0	1.2853	5.0	93.4	64	67.6
	W	20.8	4.9	10.8	1.1049	5.1	97.4	59	65.0
Grand Mean	B	18.4	7.8	16.0	1.1687	4.5	89.2	65.5	69.5
	W	19.9	5.4	11.0	1.0569	4.2	89.3	62.6	71.1
C.V. (%)	B	17.1	56.0	40.8	16.3	34.3	10.8	5.2	16.3
	W	17.0	44.0	44.5	15.7	36.5	9.5	5.2	11.5

*B=Brookings. **W=Watertown

Table 11. Mean Squares from analysis of variance of eight traits in the F_2 generation at Brookings, S.D.

Source of variation	d.f.	Protein percent	Yield (gm/plant)	Plant weight (gm/plant)	Days to head
Replications	2	32.12 **	7.96	22.88	70.80 **
Genotypes	15	397.64 **	174.19 **	483.87 **	393.42 **
G x R	30	11.16 **	15.43	40.43	12.67 **
Error	804	2.62	16.33	34.78	4.73

Source of variation	d.f.	Panicle number	Height (cm)	Groat percent	d.f.	50 Groat weight
Replications	2	10.69	585.46 **	10186.54 **	1	0.166 **
Genotypes	15	43.81 **	2954.58 **	2094.31 **	15	0.480 **
G x R	30	2.06	71.58 **	513.56 **	15	0.035
Error	804	1.65	39.12	53.30	529	0.021

*Significant at .05 level. **Significant at .01 level.

Protein percent, days to head, height and groat percent showed genotype x replication interactions.

Standard partial regression coefficients for the F_2 generation are included with the F_3 data in Table 18. Fifty groat weight, days to head, plant height and number of panicles in descending order were the best factors to predict protein content.

Plant weight was the most important trait in the prediction of yield, followed by number of panicles, plant height and days to head in this sequence.

Number of Effective Factors

Estimates of the number of effective factors determining the protein content are given in Table 12, as determined by two methods. Method 1 gave a slightly larger number of effective factors as compared to Method 2. Protein content of the 'KL' x 'RX' cross seems to be controlled by one factor, whereas crosses 'AS' x 'KL' and 'AS' x 'RX' involved several effective factors.

Heritability estimates for protein are given in Table 13. These were the methods to determine heritability in the broad sense. Crosses showed considerable variation in the heritability estimates. A large amount of variation was also seen in the heritability estimates for yield (Table 14).

Table 12. Estimates of number of effective factors controlling the expression of protein content.

Population	Method 1 *	Method 2 **
AS x KL	14	8
AS x RX	19	6
SD x KL	4	4
SD x RX	15	3
AS x SD	5	1
KL x RX	1	1

* Method 1, Castle (9)

** Method 2 , Mather and Jinks (35)

Table 13. Heritability estimates of groat protein content in twelve F_2 populations grown at Brookings in 1973.

Population	Estimate of Heritability(%)	
	Method 1*	Method 2**
KL x AS	-89	--
KL x SD	41	69
KL x RX	-26	91
RX x AS	-23	87
RX x KL	-50	98
RX x SD	29	22
SD x AS	4	63
SD x KL	18	63
SD x RX	18	24
AS x SD	51	98
AS x KL	-133	96
AS x RX	-69	-48

* Method 1, Mahmud and Kramer (33)

** Method 2, Burton (5)

Table 14. Heritability estimates of yield per plant in 12 F2 populations grown at Brookings in 1973.

Population	Estimate of Heritability(%)	
	Method 1*	Method 2**
KL x AS	45	--
KL x SD	41	55
KL x RX	93	82
RX x AS	21	25
RX x KL	32	70
RX x SD	33	--
SD x AS	47	66
SD x KL	26	-52
SD x RX	35	-55
AS x SD	56	100
AS x KL	39	98
AS x RX	46	79

* Method 1 , Mahmud and Kramer (33)

** Method 2 ,Burton (5)

F_3 Generation

Cross means, grand means and coefficients of variation are given in Table 15. These were grown at two locations, Brookings, South Dakota, and Watertown, South Dakota. Protein content showed differences due to location. Differences were also observed in the yield means. Groat percentage was approximately 10 percent lower at Watertown. Plants headed approximately four days earlier at Watertown, and height was slightly increased. Genotypes were significantly different at the 0.01 level of probability in protein percent, yield, plant weight, days to head, number of panicles, height, groat percent and 50 groat weight (Table 16). Location effects were significant at the 0.05 level of probability. Genotype x replication interactions were observed for protein content, yield and groat percent. Genotype by location differences were significant for yield, days to head, number of panicles and height. Protein and groat percent showed some interaction with replication x location and genotype x replication x location.

Simple correlation coefficients are given in Table 17. Protein content showed strong negative correlation with yield, plant weight, days to head, 50 groat weight, height and groat percent. The only positive association of protein was observed with the number of panicles and awns. Yield showed a strong relationship with plant weight, 50 groat weight, height and groat percent. Awns were negatively correlated with yield.

Table 15 . Parent and cross means, grand means and coefficient of variability of the F_3 generation at Brookings and Watertown.

		Protein percent	Yield (gm/hill)	Plant weight (gm/hill)	50 Groat wt. (gm)	Panicle number	Height (cm)	Days to head	Groat percent
AS	B*	24.4	9.9	23.6	0.76	20.5	82.3	64	42.9
	W**	26.6	8.0	15.6	0.64	15.9	86.0	62	30.5
SD	B	22.2	23.0	47.8	1.01	18.6	86.0	65	69.8
	W	24.4	18.0	34.3	0.85	17.2	86.0	59	58.7
KL	B	16.1	29.6	60.7	1.05	19.2	94.7	68	70.5
	W	17.9	22.3	45.1	0.95	17.4	94.0	64	61.2
RX	B	16.6	30.6	64.7	1.20	13.4	105.1	71	71.3
	W	19.2	22.6	50.9	1.06	14.7	102.9	67	64.9
KLxAS	B	18.9	19.4	41.8	1.06	20.9	94.7	63	67.2
	W	21.7	15.4	32.6	0.93	20.0	95.5	58	46.8
KLxSD	B	18.4	25.3	53.3	1.09	18.3	91.0	69	72.4
	W	19.9	22.3	40.4	0.97	17.6	92.0	61	63.8
KLxRX	B	15.8	32.0	64.4	1.19	16.7	98.0	69	72.4
	W	16.9	22.9	47.2	1.12	17.4	97.3	64	66.7
RXxAS	B	20.1	20.5	44.7	1.10	20.3	99.4	63	63.2
	W	21.6	17.6	36.6	1.00	18.9	104.3	57	53.5
RXxKL	B	15.9	32.0	64.0	1.20	16.7	101.2	68	72.8
	W	17.1	23.3	48.2	1.12	15.9	100.1	64	64.7
RXxSD	B	18.3	30.9	65.7	1.15	17.1	99.9	67	70.2
	W	19.9	20.1	49.5	1.07	16.6	97.2	62	63.4
SDxAS	B	23.0	17.9	40.5	0.97	21.8	89.8	63	58.5
	W	25.4	13.2	29.8	0.86	20.0	95.9	58	44.3
SDxKL	B	18.3	27.3	59.1	1.13	21.5	91.2	65	71.1
	W	19.2	19.5	42.7	1.00	17.1	91.4	61	63.2
SDxRX	B	18.1	29.5	63.0	1.19	16.2	98.3	67	71.8
	W	20.6	23.3	49.4	1.06	15.6	97.8	62	63.2
ASxSD	B	22.8	15.5	33.6	0.98	18.1	86.5	65	58.7
	W	25.5	13.0	27.3	0.88	17.9	93.8	59	47.4
ASxKL	B	19.3	19.7	40.7	1.01	20.9	92.9	63	60.5
	W	21.3	16.5	36.3	0.83	21.2	97.3	59	49.4
ASxRX	B	19.4	21.8	48.9	1.09	22.0	99.9	63	59.6
	W	22.8	14.2	32.6	0.89	17.6	98.8	59	46.6
Grand $\bar{X}$	B	19.0	24.1	51.0	1.09	18.9	93.8	65.0	64.0
C.V.(%)	B	14.3	35.1	32.1	14.20	31.1	8.7	5.2	15.4
Grand $\bar{X}$	W	21.0	17.9	38.6	0.95	17.6	95.5	61.4	53.9
C.V.(%)	W	15.1	34.3	33.2	17.8	24.8	8.7	6.6	20.9

*B-Brookings. **W-Watertown.

Table 16. Mean squares from analysis of variance for F_3 generation at two locations (Brookings and Watertown)+

Source of variation	d.f.	Protein percent	Yield (gm/plot)	Plant weight (gm/plot)	Days to head
Replications	1	5.89 n.s.	9.86 n.s.	752.59 **	.05 n.s.
Genotypes	15	574.20 **	2244.76 **	9475.92 **	525.98 **
Locations	1	1260.65 **	12172.98 *	48032.21 *	6352.28 *
G x R	15	7.29 **	69.44 **	337.51 n.s.	1.20 n.s.
G x L	15	12.87 n.s.	145.59 *	380.06 n.s.	32.57 **
R x L	1	78.24 **	35.48 n.s.	17.94 n.s.	10.78 n.s.
G x R x L	15	7.76 **	57.49 *	174.75 n.s.	2.12 n.s.
Error	1319	1.71	28.45	111.52	8.02

+Continued on page 36.
*Significant at .05 level. **Significant at .01 level.

Table 16 Continued. Mean squares from analysis of variance for the F_3 generation at two locations (Brookings and Watertown).

Source of variation	d.f.	Panicle number	Height (cm)	Groat percent	50 Groat weight (gm)
Replications	1	42.43 n.s.	385.07 **	108.72 n.s.	.076 *
Genotypes	15	309.66 **	2015.59 **	6732.52 **	.989 **
Locations	1	540.90 n.s.	977.03 *	32253.03 **	4.659 n.s.
G x R	15	29.94 n.s.	39.29 n.s.	121.18 **	.020 n.s.
G x L	15	61.80 *	302.66 **	96.78 n.s.	.031 n.s.
R x L	1	270.28 **	145.55 n.s.	207.91 *	.349 **
G x R x L	15	23.08 n.s.	31.86 n.s.	194.20 **	.030 *
Error	1319	23.09	39.87	40.20	.015

*Significant at .05 level. ** Significant at .01 level.

Table 17. Simple correlation coefficients among characters in the F_3 generation.

	Protein percent	Yield	Plant weight	50 groat weight	Panicle number	Height	Days to head	Groat percent
Yield	-0.593**							
Plant weight	-0.558**	0.919**						
50 groat weight	-0.546**	0.417**	0.424**					
Panicle number	0.215**	0.127**	0.185**	-0.182**				
Height	-0.484**	0.521**	0.847**	0.402**	-0.105			
Days to head	-0.449**	0.354**	0.355**	0.206**	-0.441**	0.208**		
Groat percent	-0.578**	0.603**	0.568**	0.455**	-0.131**	0.354**	0.322**	
Awns	0.594**	-0.270**	-0.249**	-0.260**	0.350**	-0.097	-0.370**	-0.572**

** Significant at 0.01 level.

Table 18. Rank of character influence upon yield and protein content as determined on the basis of standard partial regression coefficients in the F_2 and F_3 generations.

Character		Standard partial regression coefficient	
		F_3	F_2
Dependent variable:	PROTEIN		
Independent variables :-			
	Yield	-0.2943 (1)	-0.0884 (7)
	50 groat weight	-0.2511 (2)	-0.2481 (1)
	Groat percent	-0.2036 (3)	-0.0637 (8)
	Days to head	-0.1933 (4)	-0.2436 (2)
	Plant height	-0.1504 (5)	0.2157 (3)
	Plant weight	0.0730 (6)	-0.1710 (5)
	Panicle number	0.0652 (7)	0.1972 (4)
	Awn		-0.1427 (6)
Dependent variable:	YIELD		
Independent variables:-			
	Plant weight	0.8270 (1)	0.4024 (1)
	Protein percent	-0.0951 (2)	-0.1624 (4)
	Groat percent	0.0920 (3)	0.0202 (7)
	50 groat weight	-0.0272 (4)	0.0577 (6)
	Days to head	-0.0080 (5)	0.0193 (8)
	Plant height	0.0024 (6)	-0.1650 (3)
	Panicle number	-0.0022 (7)	0.1904 (2)
	Awn		-0.0858 (5)

Standard partial regression coefficients obtained from stepwise multiple regression analysis indicated that yield was the most important factor for the prediction of protein content followed by 50 groat weight, days to head, plant height and plant weight (Table 18).

Standard partial regression coefficients to predict yield indicated that plant weight was the strongest single determinant of yield, followed by protein content and groat percent at a much lower level.

Frequency Distribution for Protein Content

Figures 1 through 6 illustrate the protein frequency distributions of F_3 progeny and parents. The progeny from the cross 'KL' x 'AS' was skewed towards the low protein parent Kelsey (Figure 1). Roxton showed the same tendency (Figure 2). Progeny from the cross 'SD' x 'AS' showed two peaks with the mean very close to the mean of the parents (Figure 3). Quite a few segregates exceed the high parent mean. The crosses of 'SD' with 'KL' and 'RX' were skewed towards the low parent in Figures 4 and 5, respectively. Roxton and Kelsey are not very different in protein content, however their progeny averaged lower in protein than either parent (Figure 6).

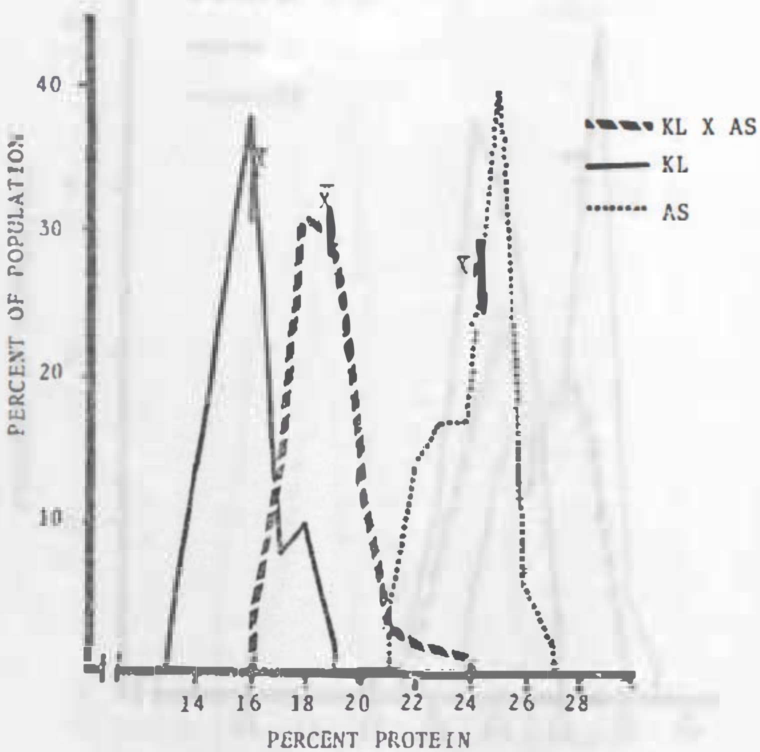

FIGURE 1. FREQUENCY DISTRIBUTION OF GROAT PROTEIN PERCENTAGES OF KELSEY,AS 6-76 and SEGREGATES(FROM F3 PLANTS)

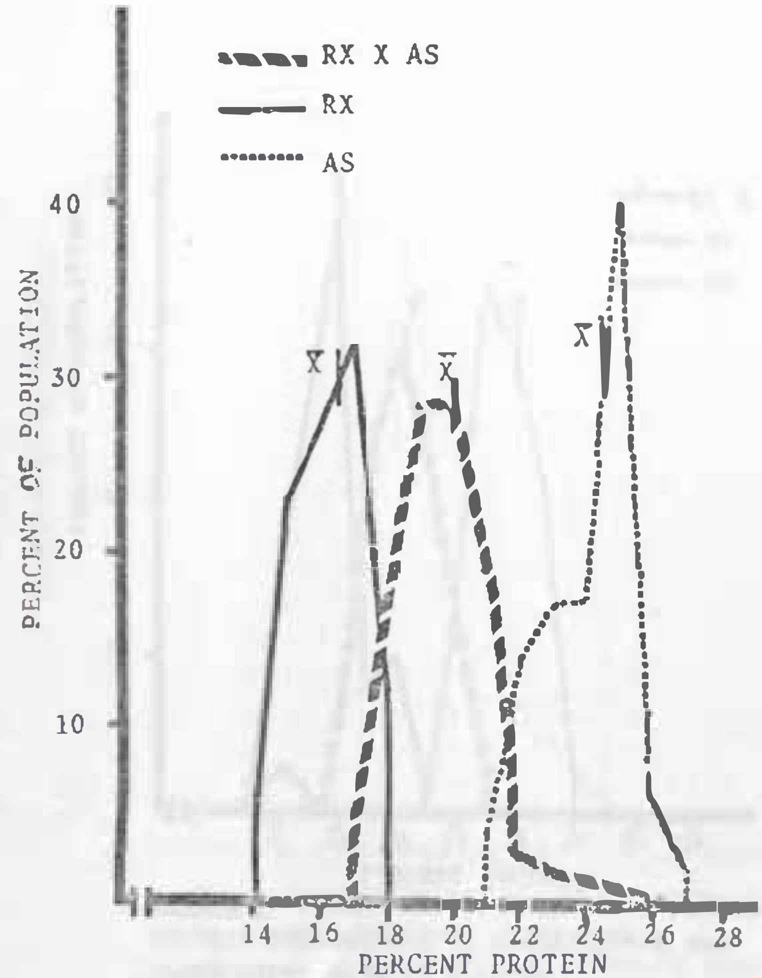

FIGURE 2. FREQUENCY DISTRIBUTION OF GROAT PROTEIN PERCENTAGES OF ROXTON,AS6-76 and SEGREGATES(FROM F3 PLANTS).

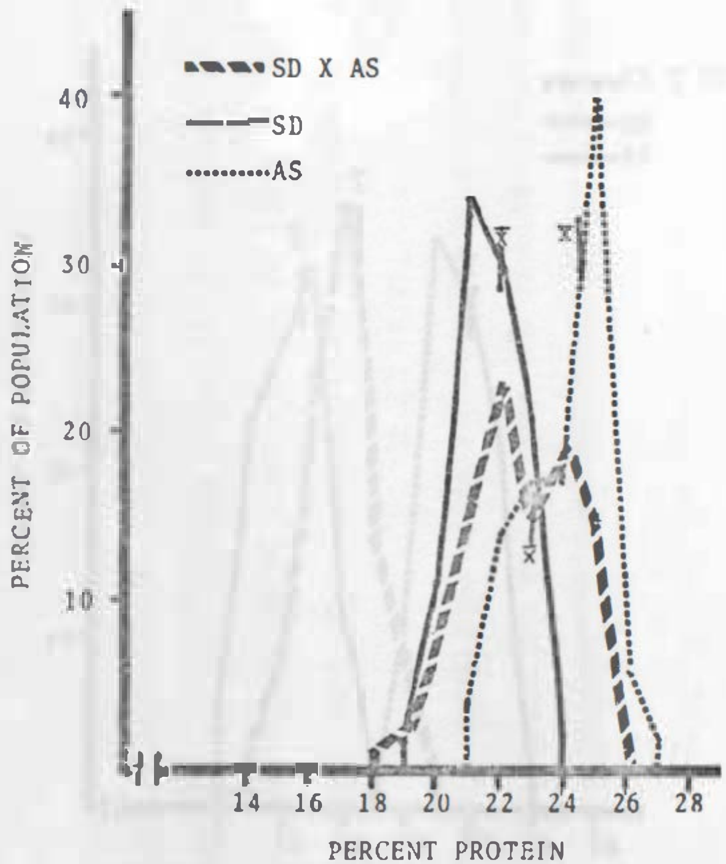

FIGURE 3. FREQUENCY DISTRIBUTION OF GROAT PROTEIN PERCENTAGES OF SPEAR,AS6-76 and SEGREGATES(FROM F3 PLANTS).

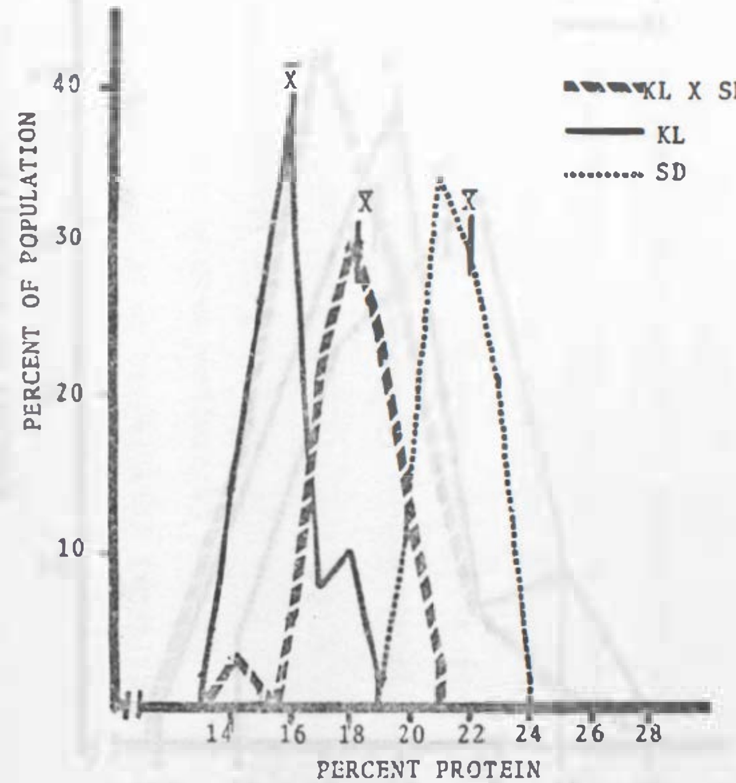

FIGURE 4. FREQUENCY DISTRIBUTION OF GROAT PROTEIN PERCENTAGES OF KELSEY,SPEAR and SEGREGATES(FROM F3 PLANTS).

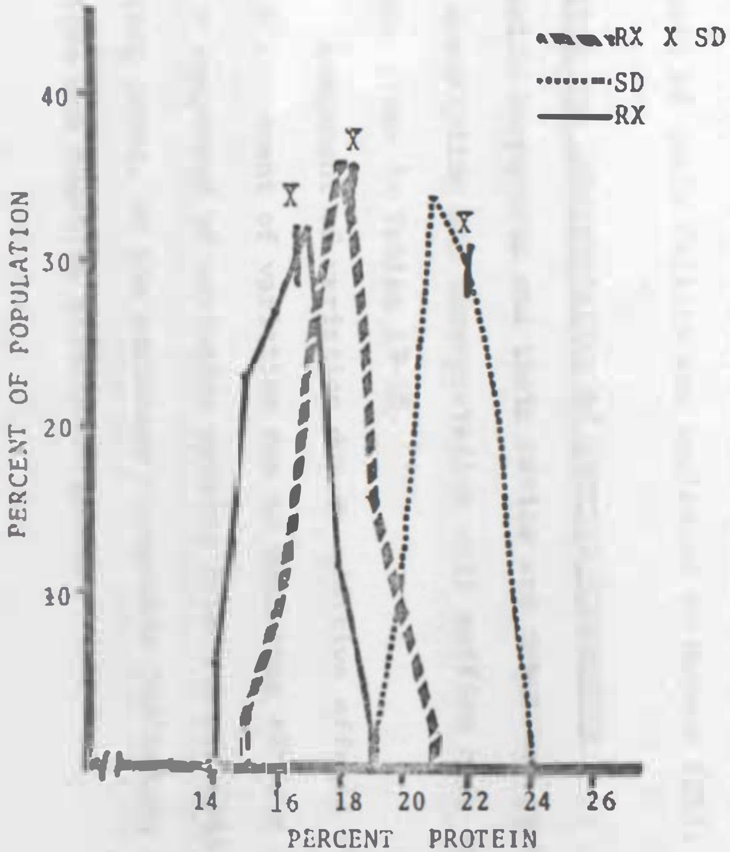

FIGURE 5. FREQUENCY DISTRIBUTION OF GROAT PROTEIN PERCENTAGES OF ROXTON, SPEAR and SEGREGATES (FROM F3 PLANTS).

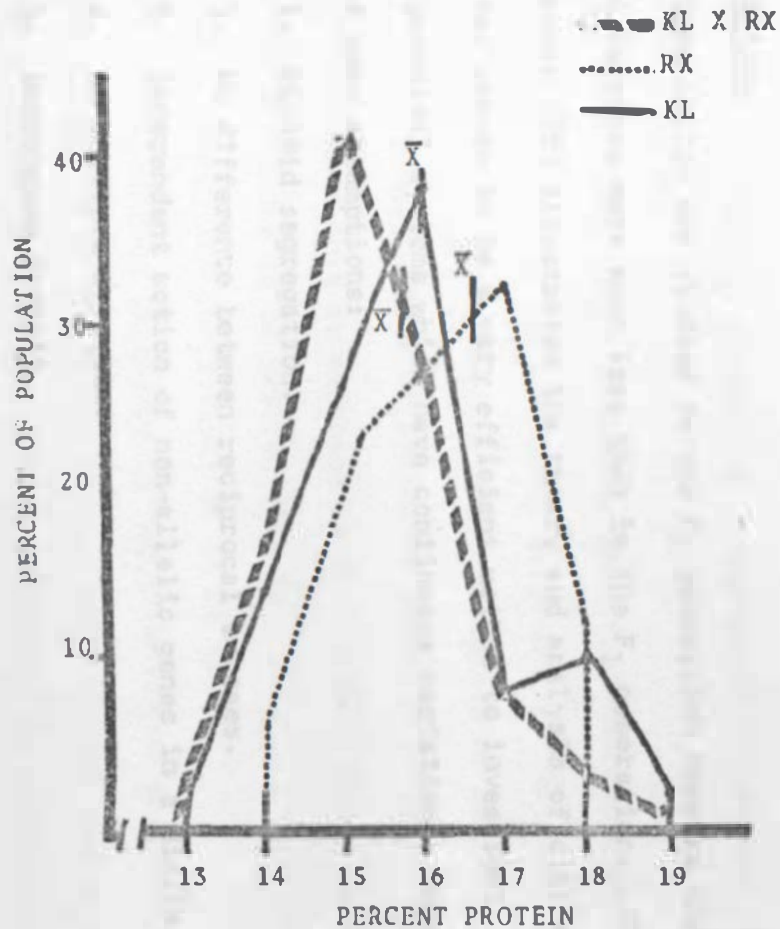

FIGURE 6. FREQUENCY DISTRIBUTION OF GROAT PROTEIN PERCENTAGES OF KELSEY, ROXTON AND SEGREGATES (FROM F3 PLANTS).

Gene Action

Gene action was studied in the F_2 generation because the reciprocal differences were much less than in the F_1 generation. Jinks (29) and Hayman (25) illustrated the theory and analysis of diallel crosses. This has proven to be a very efficient method to investigate more complex genetical systems which have continuous variation. Hayman (25) listed some assumptions:

1. Diploid segregation.
2. No difference between reciprocal crosses.
3. Independent action of non-allelic genes in a diallel cross.
4. No multiple allelism.
5. Homozygous parents.
6. Genes independently distributed between the parents.

All these assumptions are rarely met in natural populations and the effects of their failure are explained by Hayman (25).

Description and Interpretation of Genetic Components

Genetic components and their ratios are described by Hayman (25). A brief description and interpretation will suffice here for genetic components given in Tables 19-23.

D = component of variation due to additive effects of genes.

H_1 = component of variation due to dominance effects of genes.

H_2 = component of variation arising from h increments of all segregating genes, or the dominance components indicating asymmetry of positive and negative effects of genes.

F = an indication of relative frequencies of dominant and recessive alleles.

h^2 = the overall mean dominance effect of heterozygous loci.

E = the expected environmental component of variation (it measures the differences between duplicate plots or replications).

$(H_1/D)^{\frac{1}{2}}$ = mean degree of dominance over all loci. With average partial dominance this is expected to fall within the range 0-1 and with over-dominance to be greater than 1.

'b' = regression coefficient of Wr on Vr.

$H_2/4H_1$ = average frequency of negative versus positive alleles showing dominance in the parents. The value should have a maximum of one-fourth when the positive and negative alleles were equally distributed. Unequal distribution would result in a value less than one-fourth.

$\frac{Kd}{Kr} = [(4DH_1)^{\frac{1}{2}} + F]/[(4DH_1)^{\frac{1}{2}} - F]$ = the ratio of the total number of dominant to recessive alleles in all the parents.

h^2/H_2 = number of effective factors which exhibited dominance.

Heritability = this is in the narrow sense from the mean variance of arrays, Crumpacker and Allard (12).

$r(Wr + Vr)/V_2$ = the correlation between order of dominance and parental measurement.

(Vr, Wr) graph: Wr is the array variance of all offspring of each parent. In the absence of non-allelic interaction Wr is related to Vr by a straight regression line of unit slope. Vr is the variance of all the offspring of r th parent. If the model is adequate, considering assumptions of Hayman (25), this graph is a measure of the average level of dominance. The points nearest the origin stem from the arrays derived from parents with the most dominant genes and the points furthest from the origin stem from arrays derived from parents with the fewest dominant genes. The parabola $Wr^2 = V_pV_r$ delimits the area in which coordinate data (Wr, Vr) occur. The line of unit slope, b = 1, through the origin Vr, Wr is the line of complete dominance. Movement of the slope toward the left would show decreasing (partial) dominance and movement toward the right would indicate increasing dominance (overdominance). The distance between the points provides a measure of the genetic diversity of the parents.

<u>Gene Action for Protein Content</u>

The value of D was higher than H_1 and h^2 indicating additive gene action (Table 19). Asymmetry of positive and negative alleles was apparent as the value of $H_2/4H_1$ was not equal to 0.25. The negative figure for F (-3.15) and a ratio of $\frac{Kd}{Kr}$ less than 1 point out the excess of negative alleles. The heritability estimate was 83 percent.

In Figures 7 and 7A, (Vr, Wr) graph reveals the partial dominance for protein content as the position of regression is tending upward. The order of dominance at Brookings (Figure 7A) was 'SD', 'RX', 'KL' and 'AS' in replication number one and 'AS', 'KL', 'SD' and 'RX' in

Table 19. Genetic components of variation and their standard errors and ratios between components from a 4 x 4 diallel, combined over two replications, for percent protein and groat percent (Brookings).

Component	Protein percent	Groat percent
D	14.436 ±0.68	24.98 ±5.38
F	- 3.150 ±1.75	-27.23 ±13.76
H_1	- 2.046 ±1.98	-105.45 ±15.57
H_2	- 2.450 ±1.83	-68.92 ±14.37
h_2	- 2.546 ±1.24	60.83 ±9.75
E	0.488 ±0.30	21.08 ±2.39
$(H_1/D)^{\frac{1}{2}}$	0.376	2.05
$H_2/4H_1$	0.299	0.163
$\frac{K_d}{K_r} = \frac{(4DH1+F)^{\frac{1}{2}}}{(4DH1-F)^{2}}$	0.550	0.580
$h^2/H2$	1.039	-0.882
r(Wr+Vr)/Yr	0.570	0.830
'b'	0.990 ±0.33	0.78 ±0.18
Heritability	.83	.80
Magnitude and direction of dominance	= -0.425	-4.743
Order of dominance	SD RX KL AS * AS KL SD RX**	AS KL RX SD* AS RX KL SD **
Order of parental performance	KL RX SD AS	AS RX SD KL

* Replication no. 1. ** Replication no. 2.

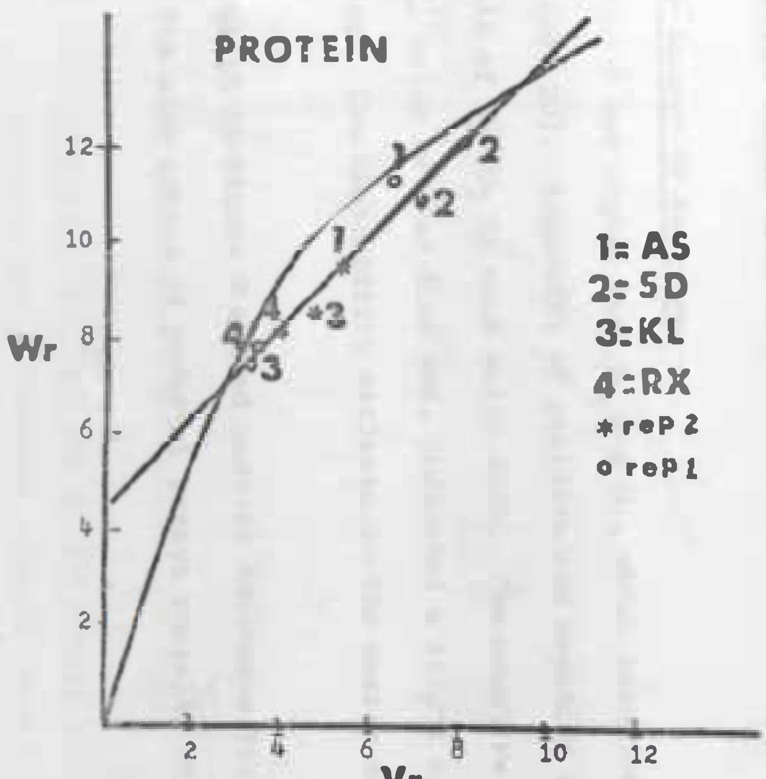

FIGURE 7. (Vr , Wr) GRAPH FOR PROTEIN IN A FOUR CULTIVAR DIALLEL OF OATS. (Watertown)

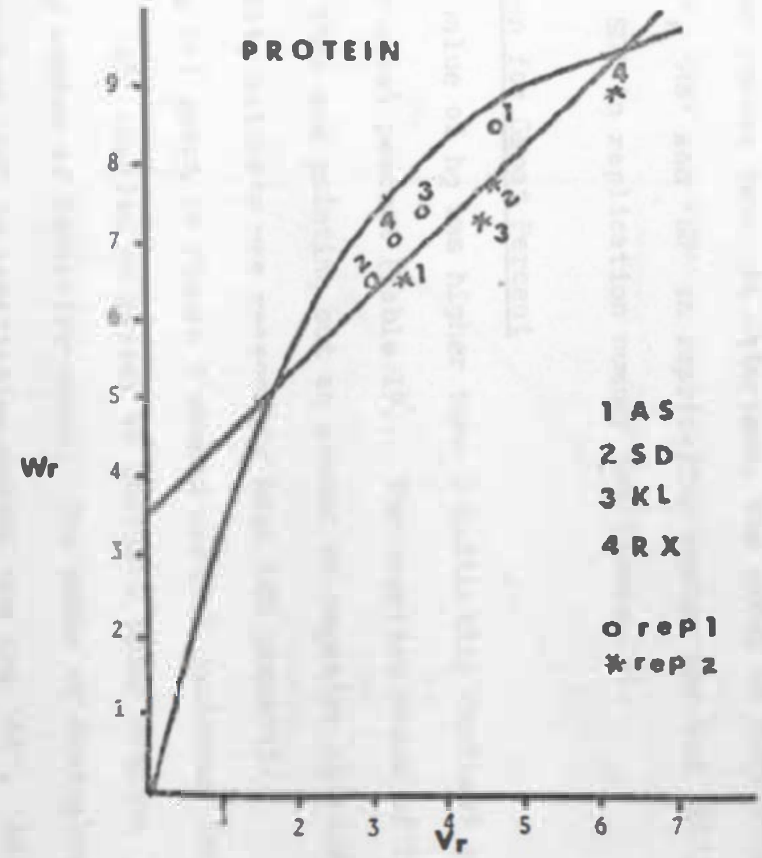

FIGURE 7A. (Vr , Wr) GRAPH FOR PROTEIN IN a 4-CULTIVAR DIALLEL OF OATS. (Brookings) replication number two. At Watertown, the order of dominance was 'KL', 'RX', 'AS' and 'SD' in replication number one and 'KL', 'RX', 'AS' and 'SD' in replication number two (Table 23).

Gene Action for Groat Percent

The value of h_2 was higher than D indicating dominant gene effects for groat percent (Table 19). The negative value of F and $\frac{Kd}{Kr}$ was less than one pointing out an excess of negative alleles. The heritability estimate was reasonably high (80 percent).

(Vr, Wr) graph in Figure 9 showed partial dominance for groat percent. 'AS' carried an excess of dominant genes whereas 'SD' had an excessive number of recessive genes. The order of dominance was 'AS', 'KL', 'RX' and 'SD' in replication number one and 'AS', 'RX', 'KL' and 'SD' in replication number two.

Gene Action for Number of Panicles

The value of D was higher than h_2 and H_1, which revealed additive gene action (Table 20). Asymmetry of positive and negative alleles was obvious as ratio of $H_2/4H_1$ is much below 0.25. The negative value of F and the Kd/Kr value of less than one, indicated a slight excess of negative alleles. The heritability estimate in the narrow sense was 81 percent.

(Vr, Wr) graph in Figure 9 showed partial dominance for number of panicles. The wide spread of parental arrays revealed broad

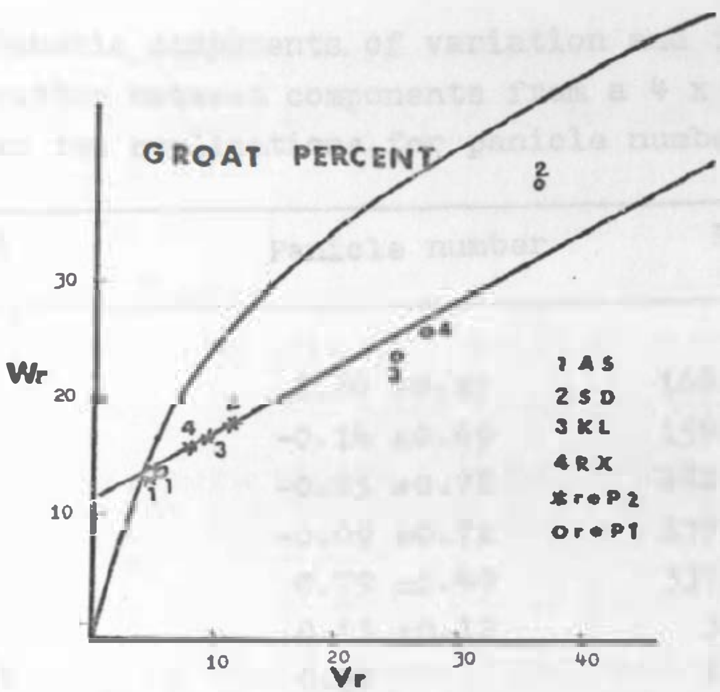

FIGURE 8. (Vr , Wr)GRAPH FOR GROAT PERCENT IN A 4-CULTIVAR DIALLEL OF OATS.

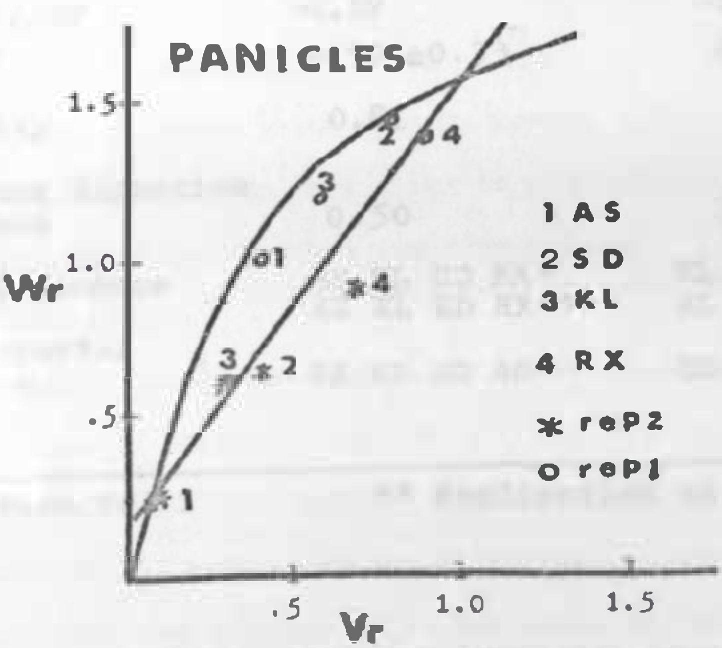

FIGURE 9. (Vr , Wr) GRAPH FOR NUMBER OF PANICLES IN A 4-CULTIVAR DIALLEL OF OATS.

Table 20. Genetic components of variation and their standard errors and ratios between components from a 4 x 4 diallel, combined over two replications, for panicle number and height.

Component	Panicle number	Height
D	1.80 ±0.27	168.28 ±7.48
F	-0.14 ±0.69	159.15 ±19.15
H_1	-0.25 ±0.78	282.16 ±21.67
H_2	-0.09 ±0.72	239.02 ±20.00
h^2	0.79 ±0.49	339.64 ±13.57
E	0.13 ±0.12	3.85 ±3.33
$(H_1/D)^{\frac{1}{2}}$	0.37	1.29
$H_2/4H_1$	0.09	0.221
K_d/K_r	0.80	2.15
h^2/H_2	-8.57	1.42
$r(W_r+V_r)/Y_r$	-0.57	-0.83
'b'	0.90 ±0.33	0.74 ±0.15
Heritability	0.81	.55
Magnitude and direction of dominance	0.50	9.16
Order of dominance	AS KL SD RX* AS KL SD RX**	KL RX SD AS* KL RX AS SD**
Order of parental performance	RX KL SD AS	SD AS KL RX

* Replication no. 1 ** Replication no. 2

genetic diversity. The order of dominance was 'AS', 'KL', 'RX' and 'SD' in replication number one and 'AS', 'KL', 'SD' and 'RX' in replication number two.

Gene Action for Plant Height

The values of h_2 and H_1 were higher than D, which implied dominant gene action (Table 20). The ratio $H_2/4H_1$ suggested an equal distribution of positive and negative alleles. The heritability estimate was 55 percent.

(Vr, Wr) graph in Figure 10 showed partial dominance as the regression line moved upward. The order of dominance was 'KL', 'RX', 'SD' and 'AS' in replication number one and 'KL', 'RX', 'AS' and 'SD' in replication number two. 'SD' and 'AS' seemed to carry excess amounts of recessive genes for height.

Gene Action for 50 Groat Weight

H_1 and h_2 had a higher value than D, revealing dominant gene effect (Table 21). $H_2/4H_1$ data were close to 0.25 which pointed out equal distribution of negative and positive alleles. The heritability estimate was 24 percent.

(Vr, Wr) graph in Figure 11 depicted over-dominance for 50 groat weight. The order of dominance was 'RX', 'SD', 'KL' and 'SD', as in replication number two. 'RX' carried excessive amounts of dominant genes whereas 'AS' had excess amounts of recessive genes. In Figure 11A the parent 'AS' was omitted, as it had shown excessive deviation

Table 21. Genetic components of variation and their standard errors and ratios between components from a 4 x 4 diallel, combined over two replications, for 50 groat weight and days to head.

Component	50 Groat weight	Days to head
D	0 .029 ±0.003	18.21 ±2.06
F	0.016 ±008	13.38 ±5.31
H_1	0.099 ±010	39.48 ±6.01
H_2	0.091 ±009	35.70 ±5.55
h^2	0.152 ±006	30.43 ±76
E	0.002 ±001	0.633±0.92
$(H_1/D)^{\frac{1}{2}}$	1.83	1.47
$H_2/4H_1$	0.229	0.226
Kd/Kr	1.660	1.664
h^2/H_2	0.24	0.852
r(Wr+Vr)/Yr	-0.93	0.88
'b'	0.80 ±0.27	1.20 ±0.23
Heritability	.24	.39
Magnitude and direction of dominance	.197	-2.47
Order of dominance	RX SD KL AS* RX KL SD AS **	AS SD KL RX * AS SD KL RX**
Order of parental performance	AS SD KL RX	SD AS KL RX

* Replication no. 1 ** Replication no. 2

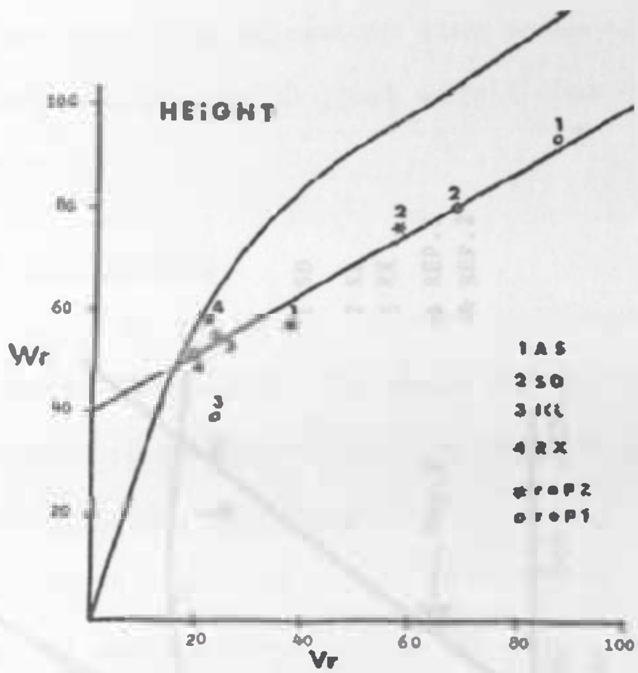

FIGURE 10. (Vr , Wr) GRAPH FOR PLANT HEIGHT IN A 4-CULTIVAR DIALLEL OF OATS.

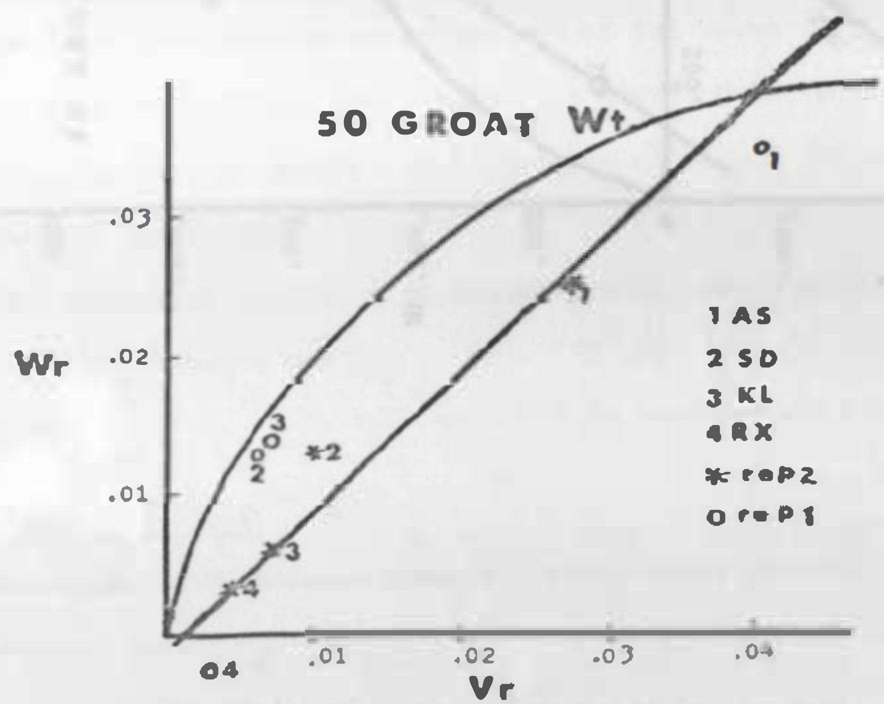

FIGURE 11. (Vr , Wr) GRAPH FOR 50 Groat weight in a 4-CULTIVAR DIALLEL OF OATS.

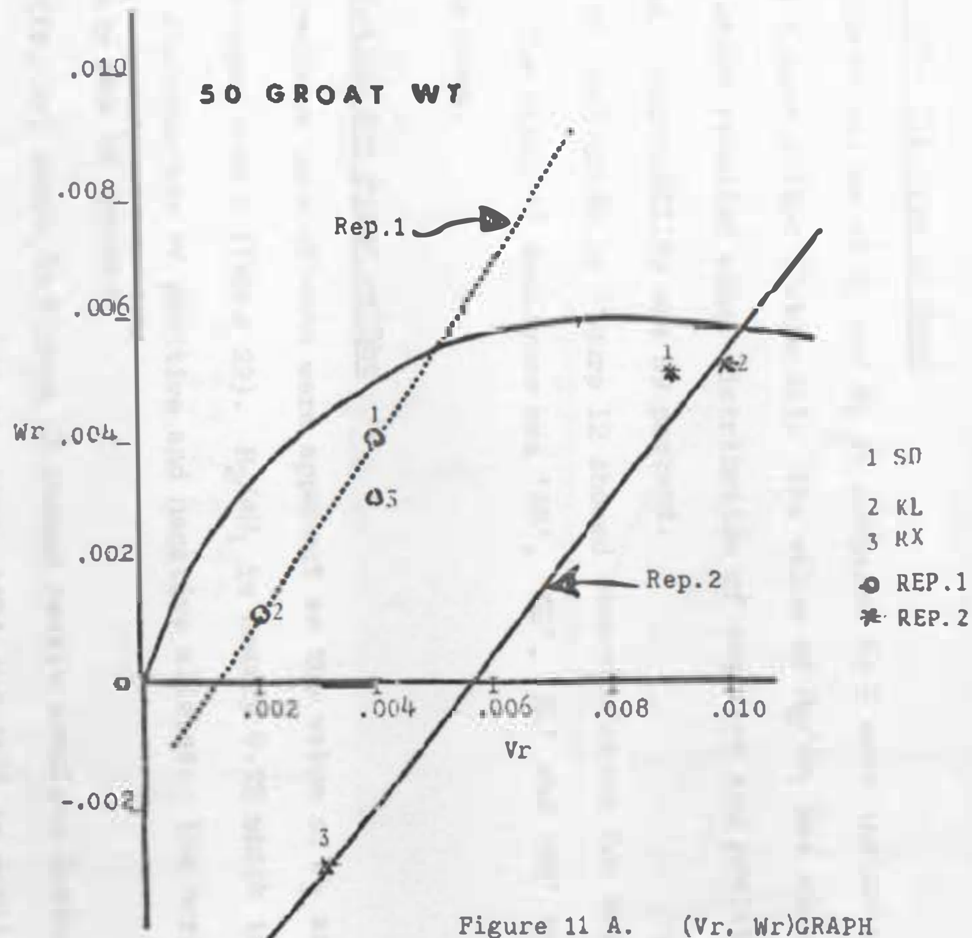

Figure 11 A. (Vr, Wr)GRAPH FOR %) GROAT WEIGHT IN A 4-CULTIVAR DIALLEL OF OATS.

from the other parents. The regression line moved to the right and pointed out over-dominance for 50 groat weight when only A. sativa parents were used.

Gene Action for Days to Head

Higher values of H_1 and H_2 as compared to D were indicative of dominant gene effect (Table 21). The value of $H_2/4H_1$ was close to 0.25, which revealed equal distribution of negative and positive alleles. Heritability was 39 percent.

(Vr, Wr) graph in Figure 12 showed over-dominance for days to head. The order of dominance was 'AS', 'SD', 'KL' and 'RX' in both replications.

Gene Action for Plant Weight

Dominant gene effects were apparent as the value of H_1 and h_2 were higher than D (Table 22). $H_2/4H_1$ is nearly 0.25 which indicated equal distribution of positive and negative alleles. The heritability estimate was 24 percent.

(Vr, Wr) graph in Figure 13 showed nearly complete dominance. The order of dominance was 'KL', 'RX', 'SD' and 'AS' in replication number one and 'RX', 'KL', 'SD' and 'AS' in replication number two.

Gene Action for Yield

The value of D is lower than H_1 and h_2 which pointed out dominant gene effect (Tables 22 and 23). But in Figure 14, which showed F_3

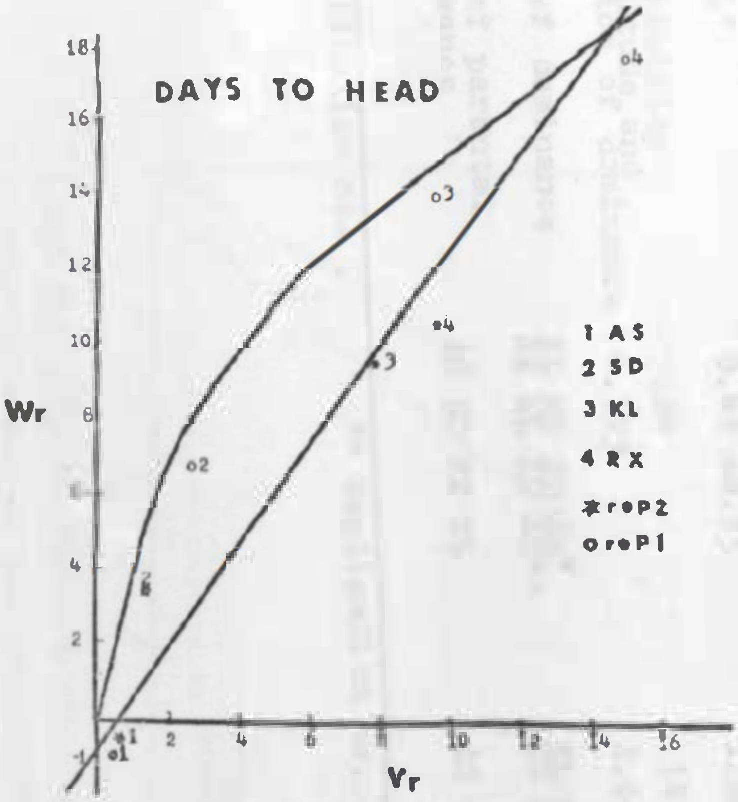

FIGURE 12. (Vr , Wr) GRAPH FOR DAYS TO HEAD IN A 4-CULTIVAR DIALLEL OF OATS.

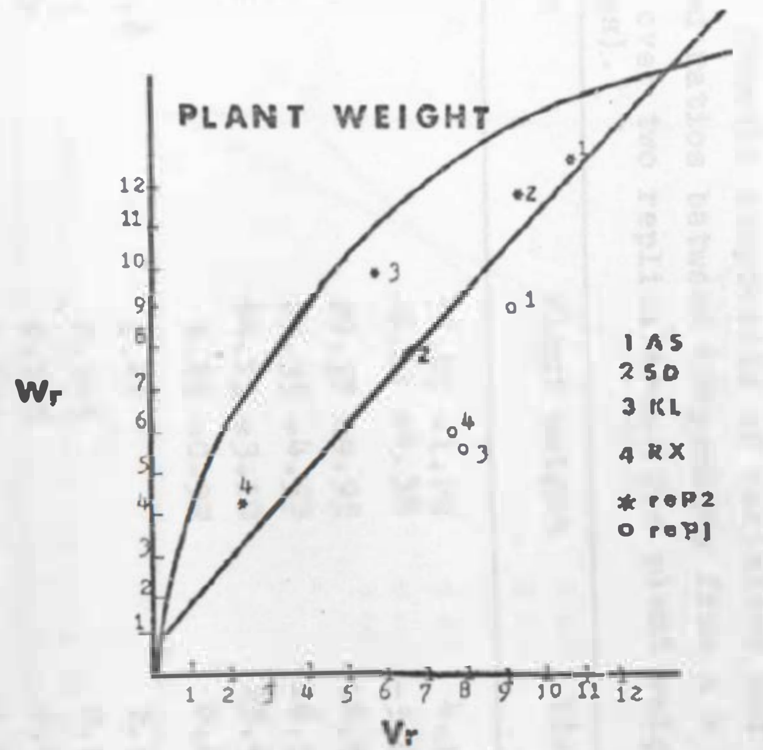

FIGURE 13. (Vr , Wr)GRAPH FOR PLANT WEIGHT IN A 4-CULTIVAR DIALLEL OF OATS.

Table 22. Genetic components of variation and their standard errors and ratios between components from a 4 x 4 diallel, combined over two replications, for plant weight and yield (Brookings).

Component	Plant weight	Yield
D	14.01 ±1.70	4.14 ±0.76
F	-6.11 ±4.38	-5.64 ±1.96
H_1	29.57 ±4.95	16.64 ±2.22
H_2	29.35 ±4.57	16.35 ±2.04
h^2	64.15 ±3.10	25.48 ±1.39
E	2.21 ±0.92	0.66 ±0.34
$(H_1/D)^{\frac{1}{2}}$	1.45	2.003
$H_2/4H_1$	0.248	0.245
Kd/Kr	0.738	0.493
h^2/H_2	2.185	1.558
r(Wr+Vr)/Yr	-0.88	-0.86
'b'	0.42 ±0.85	1.22 ±0.42
Heritability	.24	.14
Magnitude and direction of dominance	4.193	2.606
Order of dominance	KL RX SD AS* RX KL SD AS**	KL RX SD AS* SD KL AS RX**
Order of parental performance	AS SD RX KL	AS SD KL RX

* Replication no. 1 ** Replication no. 2

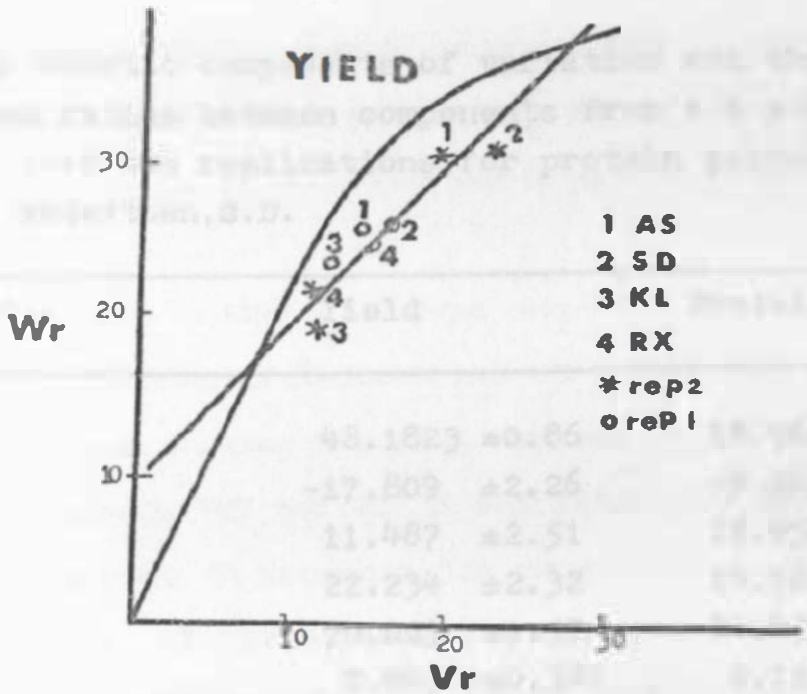

FIGURE 14. (Vr,Wr) GRAPH FOR YIELD IN A 4-CULTIVAR DIALLEL OF OATS (WATERTOWN).

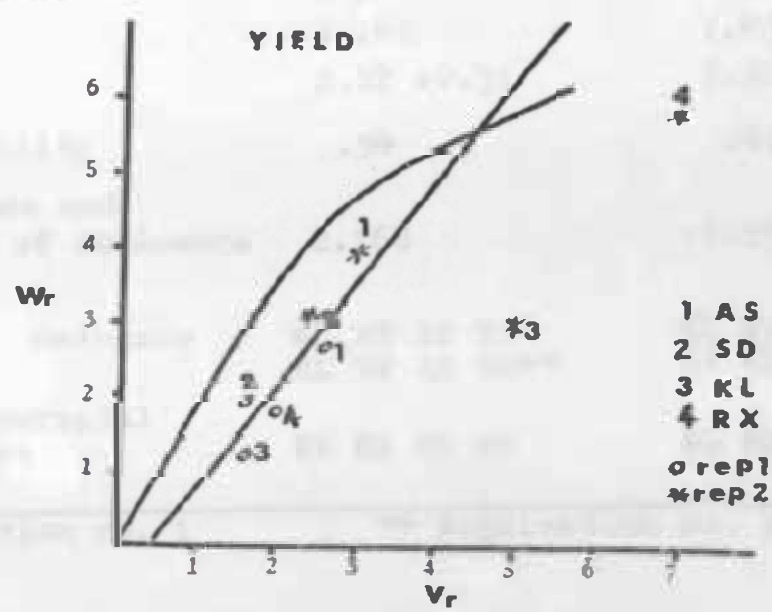

FIGURE 14.A. (Vr , Wr) GRAPH FOR YIELD IN A 4-CULTIVAR DIALLEL OF OATS (BROOKINGS).

Table 23. Genetic components of variation and their standard errors and ratios between components from a 4 x 4 diallel, combined over two replications, for protein percent and yield grown at Watertown, S.D.

Component	Yield	Protein percent
D	48.1823 ±0.86	18.062 ±0.286
F	-17.809 ±2.26	-9.205 ±0.734
H_1	11.487 ±2.51	15.953 ±0.830
H_2	22.234 ±2.32	14.766 ±0.767
h^2	70.023 ±1.57	21.436 ±0.520
E	2.843 ±0.387	0.125 ±0.127
$(H_1/D)^{\frac{1}{2}}$	0.488	0.939
$H_2/4H_1$	0.483	0.231
Kd/Kr	0.450	0.573
r(Wr+Vr)/Yr	-0.39	0.92
h^2/H_2	3.149	1.451
'b'	0.27 ±0.31	0.97±0.04
Heritability	.54	.41
Magnitude and direction of dominance	2.168	-1.173
Order of dominance	KL RX AS SD* KL RX AS SD**	KL RX AS SD* RX KL AS SD**
Order of parental performance	KL RX SD AS	KL RX SD AS

* Replication no. 1 ** Replication no. 2

yield at Watertown, the value of D was higher than H_1. Negative and positive alleles were in equal proportion. Heritability estimates were 16 percent in the F_2 generation and 54 percent in the F_3 generation at Watertown.

(Vr, Wr) graph in Figure 14A shows over-dominance for yield (Brookings). The order of dominance was 'KL', 'RX', 'SD' and 'AS' in replication number one and 'SD', 'KL', 'AS' and 'RX' in replication number two. Parents 'RX' and 'KL' in replication two showed complementary gene action. At Watertown, the pattern is very consistent (Figure 14). The order of dominance indicated was 'KL', 'RX', 'SD' and 'AS' in both replications. In Table 24, there was a constancy of generation means in the F_1, F_2 and F_3 generations. Table 25 showed the harvest indices for parents, F_2 and F_3 generations grown at Brookings and Watertown. 'AS' and 'RX' indicated comparatively lower harvest indices as compared to 'SD' and 'KL'.

Table 24. Comparative means, grand means and coefficents of variability of protein percentages in F_1, F_2, F_3 derived oat groats.

Population	F_1	F_2	F_3
AS parent	26.6	23.5	24.4
SD parent	20.5	20.7	22.2
KL parent	15.9	14.5	16.1
RX parent	15.7	15.6	16.6
KL x AS	18.4	18.7	18.9
KL x SD	16.0	17.3	18.4
KL x RX	14.7	14.5	15.8
RX x AS	18.8	19.7	20.1
RX x KL	14.5	14.6	15.9
RX x SD	17.7	17.6	18.3
SD x AS	23.7	22.6	23.0
SD x KL	16.8	17.6	18.3
SD x RX	16.7	17.8	18.1
AS x SD	25.6	21.3	22.8
AS x KL	22.7	18.8	19.3
AS x RX	20.8	19.6	19.4
Grand mean	18.4	18.4	19.0
C.V.	17.9	17.1	14.3

Table 25. Harvest indices of parents and their progenies grown at two locations in South Dakota during 1973.

Population	Harvest Index+			
	F_2 generation		F_3 generation	
	Loc. 1*	Loc. 2 **	Loc. 1*	Loc. 2**
AS parent	0.40	0.42	0.42	0.52
SD parent	0.50	0.51	0.49	0.53
KL parent	0.50	0.50	0.49	0.50
RX parent	0.44	0.46	0.48	0.45
KL x AS	0.50	0.49	0.47	0.48
KL x SD	0.51	0.53	0.48	0.56
KL x RX	0.57	0.47	0.50	0.49
RX x AS	0.45	0.44	0.46	0.48
RX x KL	0.49	0.47	0.50	0.49
RX x SD	0.49	0.50	0.47	0.41
SD x AS	0.49	0.51	0.45	0.45
SD x KL	0.51	0.52	0.47	0.46
SD x Rx	0.47	0.50	0.47	0.48
AS x SD	0.49	0.51	0.47	0.48
AS x KL	0.49	0.50	0.49	0.46
AS x Rx	0.45	0.46	0.45	0.44

* Brookings + Donald (14)

** Watertown

DISCUSSION

It is a well established principle that the progress in plant breeding is dependent on the genetic diversity in the germplasm, a reasonable magnitude of heritability and knowledge of gene action. Biometrical analysis is an excellent tool to provide genetic guidance for the improvement of quantitative traits. Complexities of such traits may be due to a large number of genes involved, unclear gene action or genotype x environment interaction. This study was undertaken to resolve the above mentioned complications and to understand the inheritance pattern of protein content and its interrelationship with other metrical traits of oats, especially yield and its components.

The parental cultivars used in this study represented a wide variation of protein content ranging from 15.7 to 26.6 percent (Table 3). 'AS' with the highest protein and fat content, was low in starch and the essential amino acid lysine (Table 2). Within the _A. sativa_ cultivars, 'SD' was highest in protein and lowest in starch content. 'KL' and 'RX' are very similar in chemical composition as well as agronomic performance. In fact, they had common ancestry with 'RX' being one of the parents of 'KL' (Table 1).

Protein and starch exhibited an interesting relationship in the parental genotypes. With the increase in percent protein, the starch percentage was decreased. The sum of these two components was approximately 70 percent. High starch parents were also higher yielders, which can be expected due to the reason that starch is the largest component in the grain. A high percent of starch may fill the grain well and make the kernel broad and plump. Shrunken kernels would be reduced in starch, thereby lower in yield. Hutchinson and Martin (26) concluded that shrunken oat kernels had higher protein content. The same trend was also observed by Ashton (1). One of the possible explanations might be that groats would have less starch, although protein remained the same. Due to the reduction of starch, the proportionate content of protein by weight might be raised. This is a limited but consistent trend in all four parental cultivars which cannot be generalized, but it may be the key point to explain the relationship between yield and protein on the grounds of chemical composition.

Another noticeable point is the effect of plant density on protein and yield. Space planted material gave about three times more yield but one percent less protein as compared to hill plots (11 plants/hill). It again depended on the genotypes. 'RX' with the smallest number of panicles did better in hill plots as compared with 'AS' with the largest number of panicles. The large number of panicles seem to compete for light, moisture and nutrients.

Protein content was very consistent from one generation to the next, as shown by the population means (Table 24). The F_1 and F_2 generations were space planted with the reduction in protein being the same as given in the preceding paragraph.

Protein content showed a significant negative correlation with yield and yield components. A similar trend was observed by Spilde (45). Data are presented in Tables 6 and 17. Protein content consistently exhibited a strong negative correlation with grain yield, number of spikelets, groat breadth (plumpness), 50 groat weight, plant weight, leaf length, width and groat percent. The positive relationship of protein content was noted with the number of panicles, groat length and awns. A large number of panicles, long groats and awns are typical features of 'AS'.

Using standard partial regression coefficients, the number of spikelets was the most influential variable to predict protein content in the F_1 generation. Yield was the number one variable in the F_3 generation to predict protein content.

Yield showed some noticeable relationships with some morphological feature of plants. In the F_1 generation the number of panicles was negatively correlated with yield and protein. Plant weight showed a significant correlation with yield ($r = 0.919$). Standard partial regression coefficients, being independent of units of measurements, allow evaluation of the relative importance of the independent variables in relation to protein content on the basis of absolute values. Plant weight in the F_2 and F_3 generations was the most influential variable to predict grain yield. Protein content, groat percentage and 50 groat weight were the other important variables to predict yield.

Heritability estimates provide a quantitative statement of the relative importance of heredity and environment determining the expression of protein content. Broad sense heritability estimates were reasonably high which gave some idea of the proportion of phenotypic variances caused by total genetic differences. Narrow sense heritability for protein content is also high, being up to 0.83. These estimates are encouraging in the breeding for high protein content. A genotype x environment interaction was indicated in all generations. According to Dudley and Moll (15) the genotype x environment interaction is the failure of differences between genotypes to be the same at different locations. The effect of significant genotype x environment interaction on genetic variances is to bias them upward, which can affect the observed variance (15).

Yield has become the number one objective in most breeding projects. Therefore it is important to understand the relationship of yield with other agronomic characters. Grafius (21) considered three components of yield in oats: number of panicles per unit area, average number of kernels per panicle and the average kernel weight. As mentioned earlier, yield was positively correlated with the number of spikelets, which is a further function of the number of grains per panicle. Another very important factor observed here is the plant weight. The significant correlation coefficient and standard partial regression coefficients support the idea that grain is directly related to plant dry matter. Donald (14) used the term "harvest index".

Harvest Index is computed by dividing grain yield by plant dry matter. He stated that grain yield can be increased either by increasing biological yield (plant dry matter) or harvest index(14). The data summarized in Table 25 exhibited very interesting relationships. 'AS' and 'RX' were the parents with low harvest index which resulted in low yield. Although 'RX' was the heaviest in plant weight, the harvest index was considerably lower than 'SD' and 'KL'. This might have resulted in the reduction in yield. There are genetic differences in the populations of different backgrounds. 'AS' indicated dominance for low harvest index and this gave rise to a reduction in grain yield. There is a possibility to develop this concept further and utilize it in plant breeding programs to raise the economic yield.

Frequency distributions for protein percentages are represented in Figures 1-6, which are nearly symmetrical. It is an indication of additive gene action. Crosses were skewed toward the low parent. Transgressive segregation for low protein was noted in Figure 6. It was also observed that some of the segregates exceeded the means of the parents in both the low and high direction. These exceptional segregates might provide an opportunity to select the desirable recombinants of yield and protein content. About 15 percent of the segregates exceeded the mid-parent values in protein content and yield.

The number of effective factors was variable depending on the genetic background of the parents involved. In the terminology of

Mather and Jinks (35), effective factors are not the genes in real sense because the effective factors are groups of genes acting together, whereas genes are the basic units of recombination. One effective factor might represent a segment of the chromosome or a cluster of genes. Crosses between 'AS' and 'RX' and 'KL' represent wide genetic variability for protein content possessing 4-19 effective factors.

Quantitative analysis for gene action is a powerful method of studying continuous variation (11). The diallel analysis described by Hayman (25) and Jinks (29) has been very useful in illustrating the gene action of eight metrical traits including protein content.

Protein content showed additive gene action in the diallel analysis. Such contention is also supported by highly significant g.c.a. and normal distribution of protein percentages. Partial dominance for protein content was exhibited. The order of parental dominance was not consistent in two replications grown at Brookings, South Dakota, in the F_2 generation. This might be due to failure of some of the assumptions mentioned at page 43. 'KL' and 'RX' indicated slight diversion from the regression line, which could have been due to complementary gene action. Figure 7 showed a very consistent pattern of parental dominance. 'KL' and 'RX' are related and indicated excessive genes. All the points are close enough on the regression line (Figure 7) and probably meet all the assumptions Hayman (25) outlined in his paper.

The groat percent exhibited dominant gene action. Partial dominance was prevalent. 'AS' carried an excessive amount of dominant genes, whereas 'SD' showed excessive amounts of recessive genes.

The number of panicles indicated additive gene action with partial dominance. The order of dominance was fairly constent with 'AS' carrying dominant genes and 'RX' carrying recessive genes. 'KL' and 'RX' were intermediate for panicle number. Dominant gene action for height with partial dominance was noticed. 'KL' and 'RX' had several dominant genes, whereas 'SD' and 'AS' possessed recessive genes.

Fifty groat weight also showed dominant gene action. Nearly complete dominance was indicated. 'AS' was totally different from the other three cultivars in groat weight. Another (Wr. Vr) graph was drawn excluding 'AS', as shown in Figure 11A. Over-dominance was seen in both replications. 'SD' manifested recessive genes and 'KL' and 'RX' exhibited dominant genes for groat weight.

Days to head had dominant gene action with over-dominance of this trait. Order of dominance was the same in both replications. 'AS' carried excessive amounts of dominant genes while 'KL' and 'RX' possessed an excessive amount of recessive genes for days to heading.

Dominant gene effects were apparent for plant weight. 'KL' and 'RX' were carrying most of the dominant genes, whereas 'SD' and 'AS' possessed recessive genes. Nearly complete dominance was manifested for plant weight. 'KL' and 'RX' exhibited complementary gene action.

Gene action for yield was also inconsistent in two replications grown at Brookings, South Dakota. Data from Watertown, South Dakota, was used to confirm the order of dominance as illustrated in Table 23 and Figure 14. A fairly consistent pattern was seen for order of dominance of parents. Over-dominance for yield was evidenced by the position of the regression line by using F_3 data from Watertown. 'KL' and 'RX' exhibited dominant genes, whereas 'SD' and 'AS' manifested recessive genes.

An overview of this study reveals several interesting observations which can be useful in practical plant breeding. High heritability estimates of protein content suggested that this trait can be selected from populations involving exotic parents, such as _A. sterilis_. In addition to increasing protein content, 'AS' has contributed to broaden the base of cultivated oats so far as crown rust resistance, earliness and certain morphological features are concerned.

Additive gene action for protein content is exhibited. This would mean that selection can be more effective in the latter generations.

Fairly consistent mean protein percent in the F_1, F_2 and F_3 generations would mean a chance to identify the desirable genotypes in the F_1 generation. Frequency distributions exhibited a shift toward the low protein parent.

Shattering is a recessive trait, as the F_1 genotypes did not shatter. Other _A. sterilis_ characteristics, as awns, pubescence and high protein content, segregate and show desirable recombinations. It is possible to utilize 'AS' germplasm to raise protein content, but it would be desirable to backcross to A. sativa to recover better agronomic traits.

The coefficients of variation were fairly high for yield, number of panicles and plant weight in the space-planted material. There can be several reasons for this. First, there was a large amount of genetic diversity due to interspecific crosses. Second, the space-planted material was probably influenced by different microenvironments thereby resulting in greater variability than is found in solid planted material. The coefficients of variation were considerably reduced in the hill plots. Even hill plots demonstrate inflated values of coefficients of variation as compared with rod rows (20).

In general this study has provided valuable information toward the understanding of inheritance of protein content and other agronomic traits. Further research is suggested in the direction of genotype x environment interaction and yield-protein-starch relationships.

SUMMARY

The objectives of this study were (a) to determine gene action, heritability and number of effective factors controlling protein content in oats, (b) to investigate the interrelationships of protein content with other agronomic characters, and (c) to evaluate the feasibility of utilizing _A. sterilis_ germplasm in oat breeding projects.

Four genetically distinct cultivars with protein content ranging from 15.7 to 26.6 percent were crossed in all possible combinations to make a complete set of diallel crosses. The data suggested additive gene action and partial dominance for protein content. Groat percentage and number of panicles showed overall partial dominance. Yield and days to heading indicated over-dominance, whereas height, plant weight and groat weight exhibited complete dominance. _A. sterilis_ manifested dominance for early heading, low groat percentage and a large number of panicles. It exhibited recessiveness for yield, plant weight and groat weight.

Narrow sense heritability for protein content varied from 41 to 83 percent while broad sense heritability ranged from 0 to 98 percent depending on genotype, environment and method used for computation. Genotype x environment interactions for protein content were significant.

Frequency distribution for protein content in the F_3 generation was reasonably symmetrical. Mean protein content was skewed toward the low protein content. F_3 progeny from a cross involving two low protein parents had a lower average protein percentage than either parent. Some crosses had progeny with as high as 25 percent protein and yield above the mid-parent value were observed.

Number of effective factors controlling protein content varied from 1 to 19 depending upon the method of determination and genetic diversity of the parents.

Protein content exhibited negative correlations with yield, plant weight, height, number of spikelets, groat percentage, leaf length, leaf width and days to heading. A positive correlation of protein content was observed with awns, which is a *A. sterilis* characteristics.

On the basis of standard partial regression coefficients, number of spikelets and yield were the most influential variables to predict protein content in the F_1 and F_3 generations, respectively. To predict yield, plant weight and number of spikelets were the best factors.

There was a constancy of generation means for protein content in the F_1, F_2 and F_3 generations. General combining ability, specific combining ability and reciprocal effects were significant in the F_1 generation for protein content.

Based upon this study, it can be concluded that the high protein content of *A. sterilis* can be combined with agronomic traits of

A. sativa. This might be achieved by selecting from large populations of segregating material followed by backcrossing to A. sativa to recover better agronomic traits.

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APPENDIX 1. Soil and weather data at Brookings and Watertown, S.D. during Summer 1973.

Soil test results	BROOKINGS, S.D.		WATERTOWN, S.D.	
Soil sample depth (cm.)	0 - 15		0 - 15	
NO_3-N (ppm)	21.6		23.0	
Organic matter (%)	2.7		3.7	
Phosphorus (Kg/Ha)	101.0		53.0	
Potassium (Kg/Ha)	241.0		237.0	
pH (1:1) dilution	6.8		6.6	
Soluble salts (mmho/cm)	0.52		0.90	
PRECIPITATION	cm	Deviation from normal	cm	Deviation from normal
April	1.80	-2.62	2.85	-2.30
May	4.45	-2.52	7.17	normal
June	3.05	-6.82	2.50	-6.75
July	6.35	+0.97	5.12	-1.55
TEMPERATURE	^oF		^oF	
April	42.5	-2.7	42.3	-0.9
May	53.2	-4.4	55.1	-0.9
June	66.4	-0.7	66.8	+1.1
July	70.1	-3.1	71.2	-1.1

APPENDIX 2 Frequency distribution of protein content for 4 oats parents and F3 generation(Hill plots), expressed as percent of population. (Brookings, 1973).

Population	Percent protein														
	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	$\bar{X}$
AS parent									4	14	17	17	40	6	2	24.4
SD parent							2	11	34	30	21	2				22.2
KL parent	2	14	26	38	8	10	2									16.1
RX parent		6	23	27	32	12										16.6
KL X AS				4	15	31	30	13	3	2		1				18.9
KL X SD	1	3	1	6	21	30	24	11	3							18.4
KL X RX	3	17	41	27	8	3	1									15.8
RX X AS					1	16	28	28	19	3	2		1			20.1
RX X KL	2	16	34	36	10	2										15.9
RX X SD			3	9	25	36	16	9		2						18.3
SD X AS						1	2	8	16	23	15	19	15	1		23.0
SD X KL			5	10	21	34	19	9	2							18.3
SD X RX			3	14	26	35	15	3	3							18.1
AS X SD					1	1	1	4	18	27	25	12	10	1		22.8
AS X KL				2	3	27	38	24	4	1						19.3
AS X RX		1	1	2	9	20	34	19	7	6	1					19.4

APPENDIX 3. Frequency distribution of single plants for protein content for 4 oats parents and F2 generation (Expressed as percent of population).

Population	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	$\bar{X}$
	Percent protein (interval 15.0 to 15.9 etc.)																
AS parent									6	13	16	19	22	6	18		23.5
SD parent							4	23	40	23	10						20.7
KL parent	6	30	34	20			2	2	2	2							14.5
RX parent	4	13	14	30	19	6	10	4									15.6
KL X AS				4	4	14	30	30	14	2	2						18.7
KL X SD		2	10	12	14	24	22	10	4	2							17.3
KL X RX	10	32	16	32	8			2									14.5
RX X AS					4	14	17	26	17	8	8	4	2				19.7
RX X KL	4	31	24	22	11	4	4										14.6
RX X SD			4	10	20	36	21	5		2		2					17.6
SD X AS							2		9	23	32	23	3	5	3		22.6
SD X KL			2	15	12	27	27	15	2								17.6
SD X RX		2	2	4	19	21	34	10	8								17.8
AS X SD						2		9	22	20	23	13	7	4			21.3
AS X KL					6	20	24	38	6	6							18.8
AS X RX		2				2	26	34	16	16	2	2					19.6